SYSTEMATICS OF THE HOLARCTIC BEETLE SUBGENUS *BRACTEON* AND RELATED *BEMBIDION* (COLEOPTERA: CARABIDAE)

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TABLE OF CONTENTS

Abstract 144
Introduction 144
Materials and methods 145
  Specimens studied 145
  Collecting *Bracteon* 147
  Specimen preparation and examination 147
  Genitalia 147
  Larvae 148
  Chromosomes 148
  Measurements 148
  Illustrations 149
  Terms 149
  Names of taxa 150
  Systematic procedures 151
Characterization of supraspecific taxa 151
  Genus *Bembidion* 151
    Notes on the type species 151
    Species included 151
    Diagnostic combination 152
    Description 153
    Subgenera and subgeneric groups of *Bembidion* 157
  Subgenus *Microserrullula* Netolitzky 158
  Subgenus *Pseudoperyphus* Hatch 158
  The *Odontium* subgeneric group 158
    Key to adults of the *Odontium* subgeneric group 159
  Subgenus *Ochthedromus* LeConte 159
  Subgenus *Odontium* LeConte 160
  Subgenus *Bracteon* Bedel 161
    Notes about synonymy 161
    Characterization of *Bracteon* 161
    Species included 163
    Natural history 163
    Character states of *Bracteon* 164
Species of *Bracteon* 169
  Species and subspecies recognition 169
    Species concepts 169
    Species delimitation within *Bracteon* 170
    Subspecies concepts 170
    Checklist of extant *Bracteon* taxa 170
    Key to adults of *Bracteon* 171
    Key to first instar larvae of the *Odontium* subgeneric-group 172
  Accounts of species of *Bracteon* 173
    Bembidion balli Lindroth 173
    Bembidion foveum Motschulsky 174
    Bembidion argenteolum Ahrens 176
    Bembidion alaskense Lindroth 177
    Bembidion semenovi Lindroth 179
    Bembidion stenoderum Bates 179
    Bembidion carinula Chaudoir 180
    Bembidion velox (Linné) 182
    Bembidion lapponicum Zetterstedt 183
    Bembidion punctatostriatum Say 185
    Bembidion hesperium Casey 186
    Bembidion lorquinii Chaudoir 187
    Bembidion zephyrum Fall 188
    Bembidion levettei Casey 190
    Bembidion inaequale Say 191
    Bembidion litorale (Olivier) 193
    Bembidion conicolle Motschulsky 194
Phylogeny of *Bracteon* 195
  Introduction 195
  The phylogenetic context of *Bracteon* 196
  Cladistic structure of *Bracteon* and related *Bembidion* 197
    Methods 197
    Choice of characters 198
    Hypothesizing transformation networks 198
    Character weighting 198
    Traditional analysis 199
    Algorithmic analysis 201
    Discussion 205
  Fossil material 207
General patterns of evolution in *Bracteon* 208
  Evolution of mirrors 208
  Evolution of larvae 209
Historical movements of *Bracteon* lineages 209
Conclusions 211
Acknowledgments 211
Literature cited 212

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ABSTRACT. A review of the Holarctic subgenus *Bracteon* Bedel (=*Chrysobracteon* Netolitzky) of the genus *Bembidion* Latreille reveals seventeen valid species (six Palearctic, eight Nearctic, and three Holarctic). The names *B. colvillense* Lindroth and *B. alaskense* Lindroth are newly synonymized, as are *B. uenoshiba* Jedlička and *B. stenoderum* Bates. *B. levettei carrianum* Casey is resurrected as a northern and eastern subspecies of *B. levettei* Casey, while the subspecies *B. inaequale opaciceps* Casey is no longer recognized.

On the basis of a detailed study of structure of adults and larvae, *Bracteon* is grouped with the subgenera *Odontium* LeConte (synonym: *Cylindrobracteon* Netolitzky) and *Ochthedromus* LeConte to form the *Odontium* subgeneric group. *Ochthedromus* and *Odontium* are briefly characterized; within *Ochthedromus*, an eastern form of *B. bifossulatum* LeConte is recognized as *B. bifossulatum cheyennense* Casey.

For adults, keys are provided to subgenera of the *Odontium* subgeneric group, and for species of *Bracteon*. For known first instar larvae, a key is provided to species of the *Odontium* subgeneric group.

States of 85 characters are described for *Bracteon*, nineteen additional species of the *Odontium* subgeneric group, nineteen other *Bembidion* species, and *Asaphidion alaskanum* Wickham. Adult structural characters, including male and female genitalia, as well as larval and chromosomal characters are studied. Some phylogenetic relationships within *Odontium*, *Ochthedromus*, and *Pseudoperyphus* Hatch are proposed using these characters; the traits also serve as evidence for the phylogenetic analysis within *Bracteon*.

A phylogeny of *Bracteon* is inferred, using both traditional (non-numerical) and algorithmic (numerical) parsimony analysis. I conclude, tentatively, that *Bracteon* is monophyletic. Contradictory evidence suggests that three species related to *B. argenteolum* are actually more closely related to a group of *Odontium* species including *B. aenulum* and *B. fusiforme* than they are to other *Bracteon*. In addition, *B. balli* and *B. foveum* may not belong with the remainder of *Bracteon*.

Almost all of the larval evolution within the group is clustered within one clade, whereas external traits of adults and genitalic features exhibit more uniform change throughout *Bracteon*. A possible correlation between female ovipositor length and size of eggbursters in larvae is noted.

Widespread dispersal and resulting sympatry of these lowland beetle taxa obscures past vicariant events. This, combined with the lack of resolution in the inferred phylogeny, creates difficulty in inferring past biogeographic events. A brief discussion of historical geographic movements of lineages is presented.

INTRODUCTION

On bare sand beaches of northern lakes and rivers, small carabid beetles, whose intricately microsculptured surfaces reflect silver and gold, scamper in the bright sunlight of warmer days. These silver-spotted beach beetles are members of *Bracteon*, a Holarctic subgenus of the large and worldwide genus *Bembidion*.

The first of seventeen known *Bracteon* species to receive a name was *Bembidion velox*, described by Carl von Linné in 1761. Since then, nearly sixty formal names have been applied to members of *Bracteon*. The Palearctic fauna was first comprehensively studied by Netolitzky (1940, 1942, 1943) and Lindroth (1940). Lindroth's later (1962, 1963, 1965) examination of world *Bracteon* included the first review of all known Nearctic species; his work forms the foundation for present worldwide studies of the subgenus.

Netolitzky and Lindroth provided descriptions of external adult structure and male genitalia of the species of *Bracteon* that they recognized. For the most part, I confirm their conclusions on delineation of extant species, and expand their study of character systems to include female genitalia and chromosomes. In addition, I extend Andersen's (1966) work on Palearctic *Bracteon* larvae, describing larvae of all eleven Nearctic species.

This character analysis serves not only to help delimit species, and provide aids for their identification, but also to supply the evidence for the primary purpose of this work: the study of evolution of members of the subgenus.

A necessary background for such investigations is the placement of *Bracteon* into its phylogenetic context; that is, a deciphering of relationships of the subgenus to other carabids. I have therefore examined the cladistic structure of the near-relatives of *Bracteon*. I present results of this preliminary work, discussing the relationships of some of the species of *Odontium* and *Ochthedromus*, groups closely related to

Bracteon. I include a redescription of the genus *Bembidion*, and notes on the subgenera related most closely to *Bracteon*, belonging to the *Odontium* subgeneric group.

The thrust of my work is the relationships of species. Present patterns within extant species, such as geographic variation, are treated only superficially. The short discussion of biogeography of the group is restricted to historical movements of lineages.

An extensive character analysis forms the core of this paper, along with a detailed examination of the phylogeny and character evolution of *Bracteon*. Separate nonnumerical and numerical analyses are presented and compared.

MATERIALS AND METHODS

Specimens Studied

About 10,100 adult, 550 first instar, 60 second instar, and 30 third instar larval specimens of Recent *Bracteon* were examined routinely; a smaller sample of specimens was studied in greater detail. Sample sizes are given for most of the data presented (Table 3). Two Pleistocene and 12 Miocene fragments were also available. About 500 Recent adults and 70 larvae of other subgenera of *Bembidion*, and of related genera, were studied as well.

Acronyms of collections from which specimens were borrowed are listed below. Also included are addresses and names of the curatorial staff with whom I corresponded. Acronyms are used throughout the text.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A. (L. H. Herman)
AMor	A. and A. V. Morgan, Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada
BCPM	British Columbia Provincial Museum, Parliament Buildings, Victoria, British Columbia V8V 1X4, Canada (R. A. Cannings)
BHar	Brian Harrison, #405-16 Lakewood Drive, Vancouver, British Columbia, Canada
BJCa	B. F. and J. L. Carr, 24 Dalrymple Green NW, Calgary, Alberta T3A 1Y2, Canada
BMNH	British Museum (Natural History), Cromwell Road, London SW7 5BD, England (N. E. Stork)
CAS	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. (D. H. Kavanaugh)
CNC	Canadian National Collections of Insects, Arachnids and Nematodes, Biosystematics Research Institute, Research Branch, Ottawa, Ontario K1A 0C6, Canada (A. Smetana)
CUIC	Cornell University Insect Collections, Department of Entomology, Cornell University, Ithaca, New York 14853, U.S.A. (Q. D. Wheeler)
DEUN	University of Nebraska State Museum, Research and Systematics Collections, W-436 Nebraska Hall, Lincoln, Nebraska 68588, U.S.A. (B. C. Ratcliffe)
DHKa	David H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.
DRMa	David R. Maddison, Department of Entomology, University of Arizona, Tucson, Arizona 85721, U.S.A.
FMNH	Field Museum of Natural History, Roosevelt Rd. and Lake

	Shore Dr., Chicago, Illinois 60605, U.S.A. (J. Keethley and J. S. Ashe)
GDND	Geology Department, North Dakota State University, Fargo, North Dakota 58105, U.S.A. (D. P. Schwert)
HNHM	Hungarian Natural History Museum, H-1088 Budapest, Baross u.13., Hungary (Z. Kaszab)
ICCM	Carnegie Museum of Natural History, Section of Entomology, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, U.S.A. (G. Ekis and R. Davidson)
ISAs	I. S. Askevold, Entomology and Biological Control, Florida A & M University, Tallahassee, Florida 32307, U.S.A.
JHAc	J. H. Acorn, Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3, Canada
JKLi	J. K. Liebherr, Department of Entomology, Cornell University, Ithaca, New York 14853, U.S.A.
JVMa	J. V. Matthews, Jr., Terrain Sciences Division, Geological Survey of Canada, Ottawa, Ontario K1A 0E8, Canada
KUSM	Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66044, U.S.A. (P. D. Ashlock)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A. (A. F. Newton, Jr.)
MNHP	Entomologie, Muséum National d'Histoire Naturelle, 45 Rue Buffon, 75005 Paris, France (H. Perrin)
OSUC	Department of Entomology, Ohio State University, Columbus, Ohio 43210, U.S.A. (C. A. Triplehorn)
OSUO	Oregon Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon 97331, U.S.A. (G. L. Peters)
ROM	Department of Entomology, Royal Ontario Museum, 100 Queens Park, Toronto, Ontario M5S 2C6, Canada (G. B. Wiggins)
SAEl	Scott A. Elias, Instaar, Box 450, University of Colorado, Boulder, Colorado 80309, U.S.A.
SMNH	Saskatchewan Museum of Natural History, Wascana Park, Regina, Saskatchewan S4P 3V7, Canada (R. R. Hooper)
TBau	Thomas Bauer collection, Universität Regensburg, Zoologisches Institut, Universitätstrasse 31, D-8400 Regensburg, Germany
UASM	Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3, Canada (G. E. Ball and D. Shpeley)
UBC	Spencer Entomological Museum, Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 2A9, Canada (S. G. Cannings)
UCB	California Insect Survey, Division of Entomology and Parasitology, University of California, Berkeley, California 94720, U.S.A. (J. K. Liebherr and J. A. Chemsak)
UMHF	Division of Entomology, Zoological Museum, University of Helsinki, N. Järnvägsgatan 13, SF-00100 Helsinki 10, Finland (H. Silfverberg)
UMSP	Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, Minnesota 55101, U.S.A. (P. J. Clausen)

UMMZ	The University of Michigan, Museum of Zoology, Division of Insects, Ann Arbor, Michigan 48109, U.S.A. (B. M. O'Connor)
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A. (T. L. Erwin and W. N. Mathis)
UWLW	Entomological Museum, University of Wyoming, Laramie, Wyoming 83070, U.S.A. (R. J. Lavigne)
ZIL	Zoological Institute, Academy of Sciences of Russia, 199164, St. Petersburg, Russia (O. L. Kryzhanovskij)
ZMLS	Museum of Zoology and Entomology, Lund University, Helgonavägen 3, S-223 62 Lund, Sweden (R. Danielsson)
ZMUM	Zoological Museum, Moscow Lomonosov State University, Herzen Street 6, Moscow K-9, Russia (N. Nikitsky)

Collecting *Bracteon*

On cloudy, cool days, *Bracteon* adults were found in cracks and burrows in sandy banks of river, creek, lake, and ocean shores. They were forced onto the surface by flooding the banks with water, and then were collected by hand; larvae were also occasionally captured by this method. On sunny and warm days, however, the beetles were active on the surface and flew if disturbed. They were caught with a net. Most adults were killed with ethyl acetate.

Most larvae were obtained using a modification of the techniques of J. Andersen and D. J. Larson (pers. comm., 1981). Adult females and males were kept in clear plastic boxes half-filled with damp, uncontaminated sand, and fed moistened pieces of Purina Puppy Chow® or Safeway Complete and Balanced Cat Food®, which were changed daily. Freshly killed insects and spiders were added on occasion. First instar larvae appeared in the sand one to eight weeks later. Some were raised to later instars on the same diet. Larvae were killed in boiling water and stored in Barber's solution or 70% ethanol. All described larvae were raised *ex ovo*.

Specimen Preparation and Examination

Wild M5® and Leitz Model RS® stereo dissecting microscopes were used to study external structures of dried adults. Permanent microscope slides were made of one or two adults of each species (except *B. semenovi* Lindroth and *B. conicolle* Motschulsky). These specimens were disarticulated and cleared, using hot 10% KOH to remove soft tissue and warm 1:1, 95% ethanol:30% hydrogen peroxide solution to reduce pigmentation, before being mounted in Euparal®. Cleared adults, genitalia, and larvae were examined using a Leitz SM-Lux® brightfield microscope at 100× or 400×. Some structures were examined with a Cambridge Stereoscan 250® Scanning Electron Microscope.

Preparation procedures for study of some characters are described in more detail below.

Genitalia

Most studied genitalia were dissected out of water-softened adults, placed in hot 5–10% KOH (aq.) for ten minutes to remove soft tissue, and then transferred via distilled water and 95% ethanol into the observation medium. Membranous portions of female genitalia were stained with chlorazol black in 70% ethanol. I examined the majority of genitalia in glycerin, except for those illustrated by line drawings, which were mounted in either Euparal® or cedarwood oil.

Some internal sacs of dried males were everted by suction (using a technique suggested by K. W. Cooper and H. Goulet, pers. comm.) after water softening and hot KOH treatment. The suction device consisted of a syringe with a thin plastic tube in place of a needle. At the end of the plastic tube was a glass capillary tube, drawn so that the internal diameter at its tip was slightly greater than the width of a *Bracteon* aedeagus. By placing this capillary tube over the apex of the aedeagus, but not over the parameres, suction could be applied to the median lobe without the whole genitalia being sucked into the syringe. The internal sac was carefully sucked out in water or weak acetic acid, then transferred to 70% ethanol for storage. The internal sacs invariably collapsed slightly after the pressure was relieved.

Most everted sacs studied were prepared by a superior technique, requiring live specimens, suggested by T. L. Erwin (pers. comm.). A live adult male was held between fingers under a dissecting scope, and gently squeezed until the genitalia and then the internal sac popped out. While being careful to maintain pressure, I grasped the specimen with a pair of forceps, and held it in boiling water for a few seconds. It was then released, and allowed to cook for about 20 seconds, the contents of the internal sac thus getting hard-boiled. The beetle was then placed in 70% ethanol for storage, or through 95% ethanol and amyl acetate in preparation for critical-point drying and SEM study. The female genitalia illustrated in Figures 185–187 were prepared by the same forced-eversion technique.

Larvae

Permanent microscope slides of cleared larvae were made by a technique similar to Goulet's (1977, 1983:226). Specimens were transferred from water through a graded series of KOH solutions into 5% KOH (aq.), which was heated to a gentle boil. After internal tissues cleared, larvae were cooled and taken through a graded series of solutions from 5% KOH down to distilled water then up to 95% ethanol; specimens were transferred with a wide-mouthed eyedropper. Larvae were placed in a weak (about 5%) solution of Euparal® in 95% ethanol, and eventually became impregnated with the mounting medium as the ethanol evaporated. To speed evaporation and prevent unwanted precipitation of Euparal, the weak Euparal solution with larvae was placed in open glass vials on a low-heat hotplate, with an electric fan close by blowing air over the vial tops. After impregnation, the larvae were mounted on slides.

Chromosomes

For most examined species, hypothesized counts and sex-chromosome systems are based on observations of male meiosis as well as male and female mitosis of Feulgen-stained squash preparations. Male and female mitoses were not observed in *B. levettei levettei*, and females of *B. lorquinii* were not studied cytogenetically. For details of the method used, see D. Maddison (1985b).

Measurements

The following measurements of adults and larvae were made using an eyepiece reticle on Wild M5® or Leitz SM-Lux® microscopes.

ADULTS:

Hl	length of head, along midline, from apex of clypeus to posterior margin of left eye
Pl	length of pronotum along midline
Pwm	maximum width of pronotum in front of hind angles
El	length of elytra, from tip of scutellum to apex
SBL	standardized body length, SBL = Hl+Pl+El

LARVAE:

LFl	length of frontale of larval head along midline
LCl	length of coronal suture
LHl	head length = LFl + LCl
LHw	width of head behind posterior stemmata

Standardized body length (SBL) is used as a measurement of overall length that is not subject to the effects of varied membrane foldings or body positions. However, there are two "standardized body length" definitions within carabid literature, because of two definitions of head length or Hl. Ball (1972) defines Hl as "straight-line distance from base of mandible to posterior margin of compound eye, on left side of head," whereas Kavanaugh (1979) treats head length as "length of head, measured along midline from apical margin of clypeus to a point opposite posterior margin of eye." Whitehead (1972), and Erwin and Kavanaugh (1981) use head length measures equivalent to Kavanaugh's. I use Kavanaugh's definition, as it is closer to the "apparent" length of the head from the neck to the apex of normally resting mandibles, and thus SBL is closer to apparent body length.

Illustrations

All drawings of beetle parts were made with a Wild M5® or Leitz SM-Lux® microscope, using a *camera lucida*, except for Figure 1, for which photographic slides were used to aid in reproducing proportions. Scanning electron micrographs were produced using a Cambridge Stereoscan 250® Scanning Electron Microscope. Photographs of cleared structures were taken with a Carl Zeiss Ultraphot II®.

Terms

The diacritical mark (!) indicates I examined the specimens being discussed.

For most structures of adults, I use terms employed by Ball and Shpeley (1983). I use "stria" in the sense of Cooper (1990). Nomenclature of elytral setae, genitalia, and larval sensilla posed some special problems, which will now be discussed. A few other terms are defined in the section "Character states in *Bracteon*," or as required in the text.

Erwin and Kavanaugh's (1981) nomenclature of setae of bembidiine elytra is used for the most part. However, within *Bracteon* there is considerably more variation in number and position of elytral setae than in most bembidiine species, making it difficult to identify homologous setae. For example, in most bembidiines, the umbilical series is constantly segregated into a humeral set of four setae (eo1 to eo4), and a subapical set of four to five setae (eo5 to eo9, Fig. 4). Within *Bracteon*, the umbilical series varies. In most specimens, two setae are present in the position of eo5 and eo6, but they occasionally number one or three. In some species, there are no umbilical setae between eo4 and eo5. In others, additional setae are present (Fig. 4), of various numbers, with as many as five setae between eo4 and eo5 on one elytron (as in the holotype of *B. semenovi*). I do not give these additional setae names (although "eo4.2," "eo4.4," and so on, could be used). I designate as eo4 the fourth most anterior umbilical seta, and eo5 and eo6 as the most posterior two setae in the position of Erwin and Kavanaugh's (1981) eo5 and eo6. The names of pre-eo4 and post-eo5 setae follow from these designations (Fig. 4).

Lindroth (1940) developed a nomenclature for male internal sac structures of several Old World species of *Bembidion*. Among species of a subgenus, Lindroth used the same name to denote homologous features. But between subgenera, no such homology is implied. Thus his "Ch1" for *Bracteon* specimens is undoubtedly not homologous to the "Ch1" of *Philochthus*. Erwin and Kavanaugh (1981) use names taken mostly from Lindroth (1940) for their treatment of the *Bembidion wickhami* (=*B. carlhi*, see Erwin [1984]) and *B. erasum* groups; indeed, the internal sac sclerites they name are probably homologous to homonymous structures shown by Lindroth (1940) for *Philochthus*. From my meager investigation of the male genitalia of *Bembidion*, I cannot determine the nature of homologies between sclerites named by Erwin and Kavanaugh and those seen in *Bracteon*. Because of this, I avoid Lindroth's and Erwin and Kavanaugh's letter and number codes, and use instead descriptive names (Figs. 99–102). These are discussed in more detail later, in the characterization of *Bracteon*.

Names of parts of beetle spermathecae vary from author to author, so that discussion of structure of these organs becomes difficult. I have chosen to follow Howden (1976) and Gordon (1985) in calling the basal bulb, near the attachment of the spermathecal duct, the nodulus; the area of attachment of the spermathecal gland, the ramus; the portion protruding beyond the ramus, the cornu (Fig. 165).

Notation of most larval sensilla follows that proposed by Bousquet and Goulet (1984). Their system works very well for *Bracteon;* that is, the sensilla of *Bracteon* larvae are for the most part in about the same positions as figured by Bousquet and Goulet (1984). I have encountered two difficulties in using their nomenclature. First, they name only setae and flat, circular sensilla of the exterior surface (their "pores"). Their system does not include hypopharyngeal sensilla, nor most sensilla on the apical articles of the maxillary palp, galea, and labial palp, and apical two antennomeres. While this is a limitation of their system, it does not diminish the excellent foundation they provided. The second difficulty is in the division of the names into two groups, one (a two-letter uppercase sclerite or organ code as well as an arabic number) for setae, and the other (a two-letter uppercase sclerite or organ code as well as a lowercase letter) for "pores." This division is based not on study of function, nor detailed electron microscope study of structure, but rather on appearance under a light microscope. Most of the "setae" in their system are probably trichoid sensilla, and most of the "pores" are probably chordotonal organs, but there are exceptions. For example, the "pore" FR_f (Figs. 194, 204) is most likely a contact chemoreceptor. Bousquet and Goulet's (1984) nomenclature may need to be revised, but for now I will use it; however, I will avoid the word "pore" for any small sensillum.

Names of Taxa

Numerous names given to members of *Bracteon* have primary types deposited in collections in Europe. I have examined few of these, and instead rely on Lindroth's (1962, 1963) interpretation of types and names. As his concepts of the species of *Bracteon* were almost identical to mine (only a few of our placements of specimens differ), I doubt that reexamination of the types he studied is crucial at present. However, Lindroth (1962, 1963) did not consider some early (pre-1961) names, as he thought they were described as mere aberrations, and did not study types of these names. Some of these were originally described as varieties, and are available names (International Code of Zoological Nomenclature [ICZN], Third edition, Article 45[g]). I list all of these names, including those clearly of infrasubspecific rank, and note those I consider unavailable. As well, primary types of some *Bracteon* names where thought by Lindroth to be lost. I make no effort to locate these types, nor to designate neotypes. Work in European museums is necessary before this can be accomplished.

For primary types that I have seen, I provide a description of the labels present with the specimen.

Publication dates of most *Bracteon* names are not controversial, except for those described by Netolitzky (1940, 1942). Lindroth (1962, 1963) considered Netolitzky (1940) to constitute a valid publication, and thus treated the names *Litoreobracteon, Argyrobracteon,* etc., as being published in 1940; he viewed the 1942 paper as a republication. Erwin and Sims (1984) as well as Netolitzky himself (1942) appear to consider the 1940 paper as unpublished, and state the publication date of those names as 1942. Apparently only reprints of the 1940 paper were issued (Lindroth, 1962:18, and Netolitzky, 1942: 29). If those reprints were distributed, then the paper does constitute a valid publication (ICZN, Third edition, Article 8). A search of North American libraries by the University of Alberta discovered not one copy; a search by Lund University of major western European libraries came up with similarly negative results (L. Cederholm, pers. comm.). However, the work was publicly distributed, at least to some extent, as a library in Chernovsti, Ukraine, possesses a copy (L. Cederholm, pers. comm.), and as Aleš Smetana (Ottawa) possesses a copy (Y. Bousquet, pers. comm.). I will therefore consider the work to constitute a valid publication.

Systematic Procedures

Methods used for inferring species limits are described later, in the section on "Species of *Bracteon*" under "Species and Subspecies Recognition." Techniques used to infer the phylogeny and biogeography of *Bracteon* and its relatives are discussed in the sections about phylogenetic and biogeographic analysis of *Bracteon*. Although the results of phylogeny reconstruction are used as part of the foundation for the supraspecific classification that follows, I defer discussion of the phylogeny reconstruction until the classification is presented and the species are described.

CHARACTERIZATION OF SUPRASPECIFIC TAXA

Genus *Bembidion*

Bembidion Latreille, 1802:82. (Type species *Carabus quadriguttatus* Fabricius, 1775:248 [=*B. quadrimaculatum* Linné, 1761:211], designated by Jeannel [1941:475].) (Generic synonymies given by Erwin and Sims, 1984.)

Notes on the type species

The originally included nominal species are *B. biguttatum* (Fabricius) and *B. quadriguttatum* (Fabricius) (Latreille, 1802), and thus one of these nominal species must serve as the type species of the genus (ICZN, Third edition, Article 69). Andrewes's (1935) designation of *B. quadrimaculatum* is therefore invalid. As he did not explicitly state that he considered *B. quadriguttatum* Fabricius to be a synonym of *B. quadrimaculatum* Linné (as is now believed [Jeannel, 1941; Lindroth, 1974a]), his designation does not constitute a fixation of the former as type species (ICZN, Third edition, Article 69[a][v]). Jeannel's (1941) statements do, however, constitute a valid designation, which is ironic considering his preference for *B. biguttatum* as the type (Jeannel [1941:475–476, footnote]). The recognition of *B. quadriguttatum* rather than *B. quadrimaculatum* as the type should not alter existing nomenclature so long as they are considered synonymous or are considered to belong to the same subgenus.

Species included

I follow Netolitzky (1942, 1943), Lindroth (1963, 1976, 1980), and Erwin and Kavanaugh (1981) in treating *Bembidion* as a very large genus with perhaps more than a thousand species, including almost all members of the subtribe Bembidiina. I conservatively follow Erwin (1972) and Lindroth (1963, 1976, 1980) in excluding from *Bembidion* members of *Asaphidion* Gosiz, *Phrypeus* Casey, *Bembidarenas* Erwin, and *Zecillenus* Lindroth; all other Bembidiina are included within the genus.

In contrast, Jeannel (1941) split *Bembidion* into numerous genera (17 in the French fauna alone), and several European systematists have followed suit (for example, Jeanne, 1971, and other titles in the same series; Antoine, 1955). Perrault (1981) has recently adopted an intermediate position; he splits *Bembidion* into ten genera world-wide. Unfortunately, rigorous phylogenetic studies of the lineages within bembidiines have yet to be performed, and as a result the cladistic structure of the subtribe Bembidiina as a whole is unclear. If future world-wide studies reveal distinct major lineages, it may prove best to divide *Bembidion* into a few smaller genera, as Erwin (1974) has done for tachyines. However, until *Bembidion* is better known, I think it best to retain the broad generic concept and avoid fragmentation into poorly resolved groups.

Papers dealing extensively with systematics of *Bembidion* on a local or global scale include Andrewes (1935), Antoine (1955), Basilewsky (1968, 1972), Casey (1918, 1924), Darlington (1959, 1962), Erwin (1982, 1984), Erwin and Kavanaugh (1981), Hayward (1897, 1901), Jeannel (1941, 1962), Jedlička (1961, 1965a), Kirschenhofer (1984), Kryzhanovskij (1983), Larochelle (1977), Lindroth (1940, 1945, 1954, 1955, 1962, 1963, 1965, 1974a, 1976, 1980), Müller (1918, 1926–1927), Netolitzky (1914a, 1927, 1940, 1942, 1943), Pawlowski (1974), Perrault (1981, 1982), and Schuler (1959).

Evidence for the monophyly (or lack thereof) of *Bembidion* is discussed under "The Phylogenetic Context of *Bracteon*"; here I give only a characterization of members of the genus. This is difficult, if not impossible, to do well at present, in part because of the large number of species in the taxon, but also because of the lack of knowledge of most members of *Bembidion*. I have gleaned information in the following diagnoses and description from Andrewes (1935), Netolitzky (1942, 1943), Lindroth (1940, 1963, 1976, 1980), Erwin (1982), Erwin and Kavanaugh (1981), Erwin and Sims (1984), from other cited sources, and from personal observations.

Diagnostic combination

Adults small to medium carabids. Members sharing with other Bembidiini narrow, subconical apical palpomere, lack of dorsal paraorbital groove, separation (in most species) of interval 9 setae into humeral set and apical set. Distinguished from other Bembidiini by possession of lacinia without dorso-apical setae; glossal sclerite bisetose; paraglossal lobes short to moderate in length; clypeus bisetose; elytra with striae represented as grooves, or rows of punctures, or effaced, sutural stria present, but short; recurrent elytral groove absent; seta eo9 lacking; uniperforate procoxal cavities; protibia truncate, not apically notched; protarsomere 1 of male with two rows of transversely apically dilated adhesive setae; internal sac of male aedeagus with brush sclerite.

First instar larva sharing with other Bembidiini egg bursters consisting of denticulate microsculpture on parietale or frontale, single-clawed tarsi, unarticulated urogomphi, which are fused to tergum nine. In addition, setae of dorsal surface generally distally tapered; if not tapered, then bluntly tipped, *not* tipped by two to six projections; seta PR_{13}, ME_{14}, and TE_{11} generally present, abdominal hypopleurites lacking setae; seta TA_1 in proximal one-third of tarsus; coronal suture relatively long (LCl/LHl = 0.09–0.22), not shorter than length of antennomere 1; mandible with cutting edge not denticulate (except slightly so in the two *B. umbratum* examined); galeomere 2 relatively short, less than 1.5 times as long as first article.

The subtribe Bembidiina contains four genera in addition to *Bembidion: Asaphidion, Phrypeus, Bembidarenas,* and *Zecillenus*. Adults of *Asaphidion* (Holarctic) differ from *Bembidion* in lacking visible elytral striae, possessing pubescent pronota and elytra, having 6 to 8 setae on the apex of the glossal sclerite (as opposed to the pair found in *Bembidion*), and having protarsomere 1 of males with small adhesive setae generally distributed, not arranged in two rows (Figs. 87, 89). Adults of *Phrypeus* (western North America) differ in lacking a brush sclerite on the internal sac of male genitalia. Adults of *Bembidarenas* (southern South America) can be distinguished from *Bembidion* by the presence of two pairs of clypeal setae, presence of 6 to 8 glossal setae, lack of a brush sclerite on the internal sac of male genitalia, and symmetrical parameres. Adults of *Zecillenus* (New Zealand) are distinct from *Bembidion* in lacking a brush sclerite on the internal sac of the male genitalia, in possessing a pronounced subapical elytral sinuation, and in having the basilateral pronotal seta far in front of hind angle (although this latter state is characteristic of several *Bembidion* species from Saint Helena [Basilewsky, 1972]).

Bembidion larvae are difficult to distinguish from those of related genera. Among Bembidiini other than *Bembidion*, larvae are known of only a few Tachyina (Cerruti, 1939; van Emden, 1942; Erwin, 1975; Gardner, 1938; Kirk, 1972; Perris, 1862; Stebbing, 1914; Thompson, 1979; Xambeau, 1894) and *Asaphidion* (Bauer, 1971; Boldori, 1939; Bøving, 1911; van Emden, 1942; Larsson, 1939; Raynaud, 1976a; my observations). The known tachyine larvae have seta TA_1 near or distal to middle of tarsus, in contrast to the more proximally placed TA_1 of *Bembidion*, the tachyine galeomere 2 is relatively long (about two times length of first), and the coronal suture is relatively short (shorter than antennomere 1) (van Emden, 1942; Hůrka, 1978). More differences may become apparent once tachyine larvae are studied in greater detail; sensillar characters are for the most part unexamined.

Many of the characters used by van Emden (1942) to distinguish *Bembidion* from *Asaphidion* do not hold for all species (Andersen, 1966; Hůrka, 1978). The single character considered by van Emden (1942), Andersen (1966), and Hůrka (1978) to separate the genera consistently is the size and number of the egg bursters: *Asaphidion* first instar larvae reportedly have a few large tooth-like spikes on the frontale in contrast to the numerous smaller denticles of *Bembidion* specimens. However, this character is inconstant. The microsculpture on the frontale of *Bembidion* ranges from absent (*B. carinula* Chaudoir, *B. aenulum* Hayward, and others), to low and multipointed (many species, including *B. foveum* Motschulsky, *B. bowditchii* LeConte, and others), to numerous small denticles (many species, including several *Bracteon* species), to a few large teeth (*B. interventor* Lindroth and *B. obtusum* Serville). Denticulate microsculpture is also present on the parietale, near the coronal suture, of all *Bembidion* first instars I have studied, reaching its most extreme form in *B. carinula* (Figs. 228, 234). This parietal microsculpture, as well as any found on the frontale, probably serves an egg-bursting function. First instars of both *Asaphidion flavipes* Linné and *A. alaskanum* Wickham have large frontale teeth *and* prominent denticles on the parietale (Boldori, 1939; van Emden, 1942: fig. 64; Bauer, 1971:158,159; my observations), a condition virtually identical to that found in *B. interventor* and *B. obtusum*. Other characters must thus be sought.

At least four characters can be used to distinguish first instar larvae of all 33 *Bembidion* species I have examined (those characterized in Tables 2, 4, and 5) from the one first instar *Asaphidion alaskanum* at my disposal. The *A. alaskanum* larva has: sensilla MX_{11} and MX_{12} relatively long (longer than a quarter the width of the palpomere to which they are attached; very much shorter in *Bembidion*); setae PR_{13}, ME_{14}, and TE_{11} each replaced by a patch of two to four short, thick setae; abdominal hypopleurites with one seta each (absent in *Bembidion*); most large dorsal setae not distally tapered (Fig. 225), instead tipped by a frequently crown-like arrangement of two to six projections (Fig. 195). Apically dilated and crowned setae are present as well in all instars of *A. flavipes* (Boldori, 1939; Bauer, 1971:fig. 4; personal observations), but apparently not in *A. yukonense* first instars (one specimen in the CNC, raised *ex ovo* by Henri Goulet, examined). I cannot yet judge the uniformity of *Asaphidion* with respect to the first three characters. The diagnosis of *Bembidion* larvae given above is thus tentative.

Description

In the following description of *Bembidion*, I include a number of previously unstudied characters. Chief among these are characters of sensilla. Setation has long been used for taxonomic characters within carabids, but the smaller sensilla of adults have generally been neglected. There is a wealth of small receptors on the surface of carabid adults, particularly on the head (for example, see the studies on antennal sensilla by Juberthie and Massoud [1977] and Daley and Ryan [1979]). The number, position, and types of these sensilla should provide numerous characters for phylogenetic analyses. Goulet (1983), Bousquet and Goulet (1984), and Landry and Bousquet (1984) have already shown the usefulness of some sensilla of larvae for inferring phylogeny, and the same may apply to other larval sensilla and sensilla of adults. I do not by any means attempt to fully describe the sensilla of *Bembidion* specimens, nor exhaust the supply of other characters. Instead, I discuss only some of those characters that appear, based upon previous work and a preliminary examination of cleared specimens of several carabid tribes, to be potentially useful for studies of carabid phylogeny.

Adult. Adults small to medium (about 2 to 9 mm in length), generally slender, in many species with relatively narrow forebody.

Color varied, many species dark, concolorous, many others with spotted elytra, or generally pale. Appendages pale yellow to black. Most species have a metallic reflection.

Microsculpture of dorsal surface varied, ranging from close-set transverse lines, giving the surface an iridescent reflection, to granulate isodiametric sculpticells, to absent.

Two supraorbital setae. Antennomeres 3 through 11 pubescent throughout length. Clypeus with one seta near each lateral margin. Labrum with six setae dorsally near apex, more numerous shorter ones ventrally; numerous sensilla of various sorts clothe the surface of the epipharynx; with one cluster of presumed chemoreceptors in a sclerotized patch on either side of epipharyngeal hump (Figs. 24, 37). Mandible with one seta in each well-developed scrobe; basomedial brush short, not extended far apically along inner surface of mandible; numerous small sensilla, with three large sensilla on dorsal surface (visible as small open circles in Figs. 25 and 28): these may be large chordotonal organs. Digitiform sensilla (Zacharuk *et al.*, 1977; Honomichl, 1980; Guse and Honomichl, 1980; Honomichl and Guse, 1981) arranged in one row near base of last maxillary palp article; tip of maxillary palp with several kinds of sensilla (Fig. 38); three centrally convergent rows of what are probably contact chemoreceptors flanked by a few small clusters of minute sensilla and a few larger possible plate-like organs (observed: *B. balli* Lindroth, *B. foveum*, *B. carinula*, and *B. umbratum* LeConte); palpomere 3 pubescent. Stipes with two long and several shorter setae in most species. Lacinia without dorso-apical setae; dorsal surface with only one to three setal rows (Figs. 42, 43, 46–48). Galea tip with three or four sensillar types, arranged as in Figure 41 (only studied in *B. foveum*). Terminal labial palpomere without digitiform sensilla, apical sensilla similar in type, but different in distribution to those of maxillary palps (Fig. 39); palpomere 2 with two to five setae on anterior margin. Glossal sclerite with two long subapical setae. One pair of setae on the mentum and 2–5 pairs of setae on the submentum. Pronotum generally with one midlateral and one basilateral seta on each side. Generally two discal setae on elytral interval 3, although *B. quinqestriatum* Gyllenhal has one, *B. laterale* Samouelle four, and a number of species have three setae (Lindroth, 1976); occasionally on other intervals as well (especially 5 and 7); elytra not pubescent; basal setiferous pore puncture (ed1) present, as well as one or two preapical discal setae (ed6 and ed7); umbilical series of setae (in interval 9, adjacent to stria 8) in most species separated into a humeral set (eo1 through eo4) and a subapical set (eo5 through eo8); eo9 lacking (*B. foveum*, *B. argenteolum* Ahrens, *B. semenovi*, and *B. punctatostriatum* Say generally have extra setae between eo4 and eo5; *B. planatum* LeConte generally has an extra seta between eo6 and eo7; members of subgenus *Euperyphus* Jeannel generally have one extra seta in the humeral set). Procoxa without setae, mesocoxa bi- or tri-setose, metacoxa trisetose on ventral surface; pro- and mesotrochanters unisetose; metatrochanter with one ventral seta in addition to several short dorso-basal setae; protarsomere 4 in both sexes of most species with ventroapical projection with four setae, the two central of which are generally apically flattened (projection and setae are lacking in *Asaphidion*, *Phrypeus*, and *Zecillenus*); male with adhesive squamo-setae (Stork, 1980), apically dilated transversely, present in two rows on protarsomere 1, and in one to two rows on protarsomere 2. Males with two major setae on sternum seven, females with four. (In this and following descriptions, sensilla of genitalia will be described elsewhere, in the sections "Male genitalia" and "Female genitalia.")

Head prognathous, with frontal furrows variously developed, from shallow to deeply incised. Eyes generally moderate to large, and convex, although small in a few subgenera (*Amerizus* Chaudoir, *Tiruka* Andrewes, etc.). Antenna in most species slender, articles subcylindrical, slightly flattened. Clypeus with frontoclypeal suture impressed. Labrum as in Figure 24, subrectangular, with front margin entire. Mandibles (Figs. 25, 28–30) falcate; terebral margin thin and cutting, with many regularly spaced pore canals extended to mesal margin (Fig. 31); ventral groove with brush of clumped microtrichia (Figs. 29c, 30c, 32, 33); right mandible generally with distinct anterior and posterior retinacular teeth, terebral tooth, premolar, and molar; left mandible with short retinacular ridge, and distinct premolar and molar; molars on both mandibles thin, only slightly sclerotized, sharply pointed (Figs. 32, 33). Maxilla (Fig. 26) with small, subulate, subconical palpomere 4; galeomeres subequal in length (articles fused in *B.* (*Amerizus*) *wingatei* Bland); galeomere 2 with groove for reception of lacinia; lacinia in most species generalized, without microsculpture. Labium (Fig. 27) with palpomere 3 small, subulate, subconical; paraglossal lobes thin (but not nearly as thin as those of trechines), rounded; short to moderate in length; with short microtrichia; glossal sclerite broad and flat. Mentum with single tooth; epilobes usually distinct; pits of mentum absent. Mentum and submentum distinct, except in members of *Ocys* Stephens.

Prothorax with closed, uniperforate coxal cavities. Pronotal shape varied, from cordate to subcircular to trapezoidal. Mesothorax broadly connected to prothorax, with conjunct-confluent coxal cavities. Scutellum visible externally, moderate in size. Metathorax with disjunct-lobate, confluent coxal cavities.

Elytron generally with nine punctate striae, in many species effaced laterally or posteriorly; sutural stria short; recurrent groove absent, although apex of stria 5 sulcate in some species; subapical plica present (most species, Fig. 67) or absent (*B. aenulum* Hayward and *B.* sp. nr. *aenulum*, Fig. 65); if present, then as typical for carabids, a simple, curved ridge on the undersurface of the elytron below setae eo7 and eo8, in most species merged with the elytral margin.

Metathoracic wing present, full, or variously reduced; if well-developed, then wedge cell a thin triangle or absent (Fig. 74); oblongulum cell elongate.

Legs long and slender in most adults. Groove in coxa for reception of metafemur restricted to posterior margin of coxa. Protibia anisochaetous, with distinct antennal cleaner ("Grade B" [Hlavac, 1971]). Protarsus with first two to three articles slightly expanded in male, with apico-lateral projections. Unguitractor plate present, plate-like. Tarsal claws simple, untoothed.

Abdomen with wing-folding spicule patches on first and sixth abdominal sterna, as well as front of seventh.

Male genitalia with styliform parameres (Figs. 180, 181), the right smaller than the left; parameres with 1 to 5 apical setae; ring sclerite as in Figure 182. Basal bulb of median lobe with most of right wall lacking; internal sac with brush sclerite (Figs. 99–102, 107) (except in a few species of subgenera *Antiperyphanes* Jeannel and *Chilioperyphus* Jeannel [Jeannel, 1962]), often with numerous other sclerites; flagellum often present, of varied shapes. Right and left testes equally developed.

Female genitalia with sclerotized spermatheca (except in the subgenera *Synechostictus* Motschulsky, *Amerizus*, *Tiru-*

ka, *Pseudolimnaeum* Kraatz [Perrault, 1981]), connected to bursa copulatrix by spermathecal duct; duct in many species with a sclerotized base, called the sclerotized vaginal plate (in coccinellids, a similar structure is referred to as the infundibulum [Gordon, 1985]); spermathecal gland present, with subbasal portion enlarged and annulated; spermatheca lying in right side of abdomen (Fig. 145; Schuler, 1960; Erwin and Kavanaugh, 1981; Perrault, 1981). Two stylomeres, second spatulate; first stylomere (S1) asetose or setose; second stylomere (S2) with zero to five or more dorsolateral ensiform and one dorsomedial ensiform setae, in addition to two nematoid setae and several furrow peg sensilla in sensory furrow, and numerous scattered chordotonal organs. Seven to ten ovarioles per ovary (Robertson, 1961).

Nervous system with first abdominal ganglion fused to last thoracic ganglion; second through seventh abdominal ganglia fused together (Ali, 1967; I have confirmed this as well for one *B. lorquinii* Chaudoir female). Proventriculus (Figs. 188, 189) with four similar, inwardly directed lobes, each lobe with patch of stout, posteriorly directed scales at anterior end, and a tubercle-studded sclerotized lobe at posterior end; in between is a membranous region of posteriorly directed microtrichia; the exact pattern varies considerably between species (observed in *B. carinula*, *B. levettei* Casey, *B. harpaloides* Serville, and *B. wingatei*). Six oval or circular rectal sclerites, arranged in one circle around circumference of rectum (Fig. 183; observed in several *Bracteon* species, as well as *B. coxendix* Say, *B. confusum* Hayward, *B. chalceum* Dejean, *B. aeneicolle* LeConte, and *B. viridicolle* La Ferté). Prothoracic muscle M15 three-parted, with M15b connected to M15c (Baehr, 1979; see that paper for further description of prothoracic musculature). Origin of muscle M3 of female abdomen at caudal end of tergum VIII (Bils, 1976; see that paper for more information about female abdominal musculature).

Pygidial defense glands (Fig. 184) paired, consisting of a long secretory duct, large, ovoid reservoir, and a pleated exit tube exiting laterally in membranous dorsum anterior to ninth and tenth tergum. Defense secretion consisting of aliphadic ketones, higher saturated acids, and aromatic aldehydes, secreted by oozing (Schildknecht *et al.*, 1968; Moore, 1979).

Chromosomes about 24 in number (male $2n = 22+XY$ in most species); sex chromosome system XY/XX or XO/XX (Smith, 1960; Rožek, 1981; Serrano, 1981a, 1981b, 1984; D. Maddison, 1985b). Male meiosis achiasmate, lacking a typical diplotene stage (Serrano, 1981c; personal observations).

Egg. Essentially unknown; only a brief description of *B. confusum* eggs exists (Silvey, 1935).

Larva. Larva generalized, without striking modifications. The following description is based on examination of 35 species in my collection as well as the brief published descriptions of *Bembidion* larvae (Andersen, 1966; Bauer, 1975; Bøving, 1911; van Emden, 1942; Jeannel, 1941; Larsson, 1941, 1968; Kirk, 1972; Lindroth, 1955, 1980; Netolitzky, 1926; Raynaud, 1976b, 1977; Rey, 1887; Rye, 1908; Schaum, 1859; Schiødte, 1867; Silvey, 1935; Smrz, 1979; Thompson, 1979; Uéno, 1955). The description applies to first instar larvae; details about second and third instars are given later.

Size. LHw = 240–605 μm, LHl = 240–570 μm.

Microsculpture denticulate on parietale near coronal suture, probably serving an egg-bursting function (Figs. 226–231). Frontale posteriorly with microsculpture absent, or low, multitoothed combs, or consisting of numerous or few small denticles, or a few large denticles (Figs. 226–231); frontal microsculpture probably also serves an egg-bursting function.

Number and position of setae and chordotonal organs ("pores") are as inferred by Bousquet and Goulet (1984) to be ancestral carabid state, except as noted below. Frontale with extra small sensillum (Fig. 205) between or near FR$_8$ and FR$_9$; this sensillum is present in many carabids, including *Opisthius*, *Elaphrus*, *Gehringia*, *Patrobus*, *Pterostichus*, *Platynus*, and *Harpalus* larvae, and perhaps should be added to the hypothesized ancestral complement. Antenna (Fig. 201) with sensorial appendage prominent and basally constricted. Chordotonal organ MX$_c$ of maxilla (Fig. 203) equidistant from MX$_2$ and MX$_3$; setal group gMX with only one to two rows of setae; MX$_{11}$ and MX$_{12}$ very small, conical (similar to FR$_f$, Fig. 204). Digitiform sensilla on maxillary palpomere 4 arranged in one subapical row around circumference of article (Fig. 206); apical sensilla of palpomere as in Figure 206. Galea with four apical sensilla (Fig. 207), in same pattern as found in *Nebria* (Spence and Sutcliffe, 1982). Labium (Fig. 202) with LA$_5$ on glossal projection, which is therefore quadrisetose (Fig. 209); digitiform sensilla arranged irregularly laterally on apical palpomere near base (Fig. 208); apical sensilla as in Figure 208. Many long setae covered with short projections emerge from the mouth cavity over the labium (Fig. 202), similar to setae found in *Omophron* (Landry and Bousquet, 1984) and many other carabids (my observations). Chordotonal organs PR$_h$, PR$_i$, and PR$_j$ absent from pronotum. Mesothorax with chordotonal organs ME$_d$ and ME$_e$ absent. Metathorax lacking seta ES$_1$. Legs with seta FE$_2$ shorter and thinner than other setae on femur. Abdomen with TE$_b$ absent from all segments; seta TE$_3$, TE$_4$, TE$_5$ present on first segment; TE$_5$ and one of TE$_3$ or TE$_4$ absent from all other segments. First abdominal sternum with ST$_5$ absent; all sterna without setae on hypopleurites.

Head (Figs. 194, 210–217, 219–224) with postorbital groove shallow or absent, occipital groove shallow. Nasale varied, denticulate (Figs. 192, 193, 238). Six stemmata on each side (apparently absent in *B. obtusum*). Mandible (Figs. 198–200) with single retinacular tooth, and penicillus; mesal margin not denticulate anterior to retinacular tooth (except slightly denticulate in the two *B. umbratum* examined). Maxilla as in Figure 203, without remnant of lacinia; palp with three articles, none subdivided. Galeomere 2 narrow, elongate, 1 to 1.5 times length of galeomere 1. Labium as in Figure 202, palp with two articles, none subdivided; palpomere 2 elongate and narrow.

Prothorax and metathorax lacking spiracles; spiracles present on mesothorax.

Leg with only one claw.

First through eighth abdominal segments with spiracles. Urogomphus not articulated, fused to ninth tergum.

Second and third instar larvae with characters of first instar, but with setae more numerous on most body sclerites. Body sparsely covered with very short setae, in addition to the more evident, long setae. Stipes with three or four setae on outer margin. Egg bursters absent. Cervical groove more prominent than in first instars, head less constricted basally (Fig. 218). Antennae and maxillae more elongate than in first instars.

Pupa. Unknown, except for a brief published description for *B. confusum* (Silvey, 1935).

Subgenera and subgeneric groups of *Bembidion*

The genus *Bembidion* is divided into a large number of subgenera or species groups. Only a few attempts have been made to join these subgeneric taxa into more inclusive natural groups. Netolitzky (1942, 1943) recognized several divisions within *Bembidion*. Species with an angulate humeral margin (including *Bracteon*) were separated from those with an evenly prolonged or absent margin; in the latter group he proposed two major series, divided between species with ed3 and ed5 attached to stria 3 (the "*Peryphus*-Reihe"), and those with ed3 and ed5 in interval 3, unattached to a stria (the "*Notaphus*-Reihe"). Jeannel (1941) divided *Bembidion* more finely, into six phylogenetic series: the *Ocys*, *Cillenus*, *Notaphus*, *Bem-*

bidion, *Peryphus*, and *Odontium* series. The *Odontium* series contains four taxa, ranked by Jeannel as genera, namely *Phyla*, *Metallina*, *Hydrium*, and *Odontium*, linked by common possession of angulate humeral margin. His genus *Odontium* includes a number of subgenera, among them *Bracteon*, that appear closely related. I include his genus *Odontium* within *Bembidion*, and call it the "*Odontium* subgeneric group." The group comprises three subgenera from the northern hemisphere. Possibly related to it are the subgenera *Microserrullula* and *Pseudoperyphus*, which I will now briefly discuss.

Subgenus *Microserrullula* Netolitzky

Serrula Netolitzky, 1910:209 (not Mörch 1853).
Microserrullula Netolitzky, 1921:185. (Type species *Bembidion aegyptiacum* Dejean, designated by Jeannel, 1941:540.)

Darlington (1959) suggested that the Oriental-Ethiopian subgenus *Microserrullula* may be related to *Odontium*. *Microserrullula* contains about thirteen species, ranging from Laos and India north into the Caucasus, west into Africa, and as far south as Madagascar (Andrewes, 1935; Netolitzky, 1942; Schuler, 1959; Basilewsky, 1968). Members of the subgenus are characterized by a number of features, including: possession of serrulate elytral margin; prominent suborbital ridge; broad pronotal base; very long flagellum of male genitalia; long, multiply coiled spermathecal duct. Judging by the apparent uniqueness of these features within the bembidiines, they are probably derived traits.

In general appearance, *Microserrullula* specimens greatly resemble members of *Odontium*, especially with the prominent and angulate shoulder margin, large size, broad pronotum, and full elytral striae. However, I cannot clearly interpret these characters phylogenetically; genitalic character states in *Pseudoperyphus* that suggest relationship with the *Odontium* group are not present in *Microserrullula*, but the states of *Microserrullula* may simply be autapomorphies. Proper placement of the subgenus awaits more detailed study, especially of first instar larvae. *Microserrullula* may belong in this group, but I will exclude it from subsequent analyses because of the uncertainty.

Subgenus *Pseudoperyphus* Hatch

Pseudoperyphus Hatch, 1950:100. (Type species *Bembidion chalceum* Dejean, by original designation.)
Bracteomimus Lindroth, 1955:49. (Type species *Bembidion chalceum* Dejean, by original designation.)

Subgenus *Pseudoperyphus* Hatch may be closely related to the *Odontium* subgeneric group. It contains at least six North American species (*B. chalceum* Dejean, *B. antiquum* Dejean, *B. honestum* Say, *B. integrum* Casey, *B. rufotinctum* Chaudoir, and one undescribed species, herein called *B. "sp. 17"*) (D. Maddison, in preparation). Adults differ from the *Odontium* subgeneric-group by lack of an angulate humeral margin, and by possession of an exceptionally thick ventral margin of the right lobe of the central sclerite complex of the internal sac of the male genitalia. The first stylomeres of females have numerous (eight or more) long setae (as long or longer than those of *B. stenoderum* Bates, see Fig. 152), a state I have seen elsewhere only in *B. (Hirmoplataphus) concolor* Kirby. First instar larvae lack a frontal spot pattern and have a relatively unconstricted neck. Members are found on rocky shorelines. In spite of these differences, the construction of the male internal sac and spermatheca are essentially identical to those of *Bracteon* and its relatives, and some relationship may be indicated. I will discuss *Pseudoperyphus* further in my phylogenetic analyses.

The *Odontium* Subgeneric Group

Members of the *Odontium* subgeneric group are generally large *Bembidion* (SBL = 3.3 to 7.1 mm, generally over 4.5 mm), inhabiting sand or silt shores of creeks, rivers, and lakes. Internal sac of male genitalia strikingly uniform in pattern, consisting of large dorsal plate, central sclerite complex with right lobe and long flagellum, and relatively small ventral sclerite patch of two basins, as in Figures 112–128. In females, S1 is setose, without sclerotized plate at base of spermathecal duct. The humeral margin is angulate; stria 5 is not apically sulcate, with the adjacent outer interval not ridged; elytra unspotted by pigment. Larvae generally have a three-spotted frontale (Figs. 215, 216, 219), with posterior part of the wide head constricted, and short coronal suture (for the *Odontium* subgeneric group, LCl/LHl = 0.09–0.20 [excluding *B. aenulum,* 0.09–0.16], mean = 0.12 [n = 16 species, 42 specimens]; for other *Bembidion,* LCl/LHl = 0.15–0.22, mean = 0.18 [n = 16 species, 20 specimens]).

Two apparent clades within this group are generally considered distinct subgenera: *Bracteon,* with 17 species; *Ochthedromus,* with two species. The remainder of the subgeneric group is placed within subgenus *Odontium;* some authors remove from *Odontium* a collection of species including *B. striatum* (Fabricius) and *B. bowditchii* (for example, Lindroth, 1963), but I prefer to follow Jeannel (1941), and not recognize the distinction. I also include within *Odontium* the members of *Cylindrobracteon* Netolitzky, following Kryzhanovskij (1983). I will discuss these decisions further under the account of subgenus *Odontium.*

New subgeneric names could be proposed for clades such as the *B. confusum* + *B. arizonae* + *B. sculpturatum* group, but this is quite unnecessary at present and would only add unneeded names to the literature. I will not radically alter existing subgeneric classification; such changes await more detailed study of the group.

Key to Adults of the *Odontium* Subgeneric Group

1. Setae in elytral interval 3 surrounded by a distinct, dull patch, which has deeper microsculpture lines and is therefore more granulate than the rest of the elytron .... *Bracteon*

1′. Elytral interval 3 with more uniform microsculpture 2

2(1′). Setae ed3 and ed5 in elytral interval 3 in large foveae; pronotal base markedly constricted; submentum with more than eight long setae .... *Ochthedromus*

2′. Elytral intervals lacking foveae, or, if foveae present (*B. foraminosum* Sturm), then pronotum less constricted (similar to Fig. 6); submentum with six or less long setae .... *Odontium*

Subgenus *Ochthedromus* LeConte

Ochthedromus LeConte, 1848:453. (Type species *Bembidion americanum* Dejean, designated by Lindroth [1963].)

Adults of *Ochthedromus* can be distinguished by the following combination of characters: protruding eyes; submentum with transverse row of about 10 long setae, suborbital setae especially long; pronotum with constricted base, and markedly rounded sides; humeral margin angulate; elytra with foveae at bases of ed3 and ed5; punctures of striae small; male internal sac with markedly sclerotized strip inward of ostium: a similar sclerotized strip occurs in some other *Odontium* subgeneric group members, but in *Ochthedromus* specimens the strip has a papillate appearance, as if composed of numerous minute beads. Larva known of *B. bifossulatum cheyennense* Casey; with three-spotted frontale; other characters listed in Table 5.

Lindroth (1963) considered *Ochthedromus* as consisting of two species, *B. bifossulatum* LeConte and *B. americanum* Dejean. My studies indicate that *B. bifossulatum* consists of two distinct forms, separable on the basis of the mentum teeth and male genitalia. As they are important for my discussions of *Bracteon* phylogeny, a clarification of their nomenclature is warranted. The western form has a rounded, somewhat-trapezoidal, laterally ridged mentum tooth, with distinct epilobes (Fig. 58); the ostial sclerotized strip in the male internal sac is abruptly bent. The eastern form has a rectangular, truncate, bulbous mentum tooth, with somewhat indistinct epilobes (Fig. 57); males have a more gently curved ostial sclerotized strip. In the material at hand, the two forms appear allopatric. However, I have not studied much material, and further study may reveal sympatry with or without evidence of gene flow. I am uncertain as to whether to consider them separate species or subspecies; nonetheless, distinct names are warranted, and herein I will treat them as subspecies. The types of three names belong to the western form (*B. bifossulatum* LeConte, 1851 [holotype female, MCZ!], *B. regestum* Casey, 1918 [lectotype male, USNM!], and *B. ferreum* Casey, 1924 [lectotype female, USNM!]), with *B. bifossulatum* LeConte being the valid name. The types of three names belong to the eastern form (*B. cheyennense* Casey, 1918 [lectotype male, USNM!], *B. sufflatum* Casey, 1918 [lectotype male, USNM!], and *B. nuperum* Casey, 1918 [holotype male, USNM!]); I herewith choose *B. bifossulatum cheyennense* Casey as the valid name.

Taxa included in *Ochthedromus:*

B. bifossulatum bifossulatum LeConte, 1851:186. (CA, ID, BC) !

B. bifossulatum cheyennense Casey, 1918:15. (AZ, CO, WY, AB, SA, and eastward) !

B. americanum Dejean, 1831:87. (U.S.A., Canada) !

Subgenus *Odontium* LeConte

Odontium LeConte, 1848:452. (Type species *Bembidion coxendix* Say, designated by Jeannel [1941].)

Cylindrobracteon Netolitzky, 1940:159. (Type species *Bembidion fusiforme* Netolitzky, by original designation.)

Adult *Odontium* can be distinguished by the following combination of characters: with characters of the *Odontium* subgeneric group; silver spots lacking; elytra around ed3 and ed5 generally without foveae; if foveae present, then submentum with six or less long setae.

Odontium is often split into two or three subgenera, but the distinction between them seems rather slight. The *B. striatum* group has been removed because of the wide interval 9 (as wide as 8), and the shallow stria 8 in front half of the elytron (Lindroth, 1963:242), and mouthpart structure (Netolitzky, 1942:49). The elytral characters, however, are not at all clear, with several species (for example, *B. robusticolle* Hayward, *B. carinatum* [LeConte], and *B. durangoense* Bates) showing intermediate states. Figure 2 illustrates the lack of two distinct groups in the *Odontium* complex based on the relative widths of intervals 8 and 9. As well, mouthpart structure is more uniform across the group than supposed by Netolitzky: only *B. confusum*, *B. sculpturatum*, and *B. arizonae* have distinctive mandibles and laciniae. Four or five East Asian species are occasionally distinguished as a separate subgenus, *Cylindrobracteon*. The only known distinctive character of the group is the fusiform body, with pronota that are trapezodial, with broad base (extended outward to humeral angles), nearly straight margins, and protruding, almost-divergent front angles. As well, the midlateral pronotal seta is absent, and the humeral margin is long, but these latter traits are shared with a number of *Odontium* (s. str.) species. The North American species *B. aenulum* and *B.* sp. nr. *aenulum* are two such species, and their pronota are somewhat intermediate between those of *Cylindrobracteon* and other *Odontium* (s. str.). Following Kryzhanovskij (1983), I do not consider *Cylindrobracteon* distinctive enough to warrant subgeneric status. Until *Odontium* is better understood phylogenetically, I will treat the species as belonging to one subgenus.

Odontium comprises all species of the *Odontium* subgeneric group other than *Ochthedromus* and *Bracteon*. It is likely that it is paraphyletic, with *Ochthedromus* or *Bracteon* derived from it. I hesitate splitting it into monophyletic units until its parts are better known.

North American and western Palearctic members of the subgenus appear well understood (except for one undescribed species in southern U.S.A.), but material from the eastern Palearctic region is in need of study.

Note that "*Bembidion bowditchi*" is an incorrect subsequent spelling of *Bembidion bowditchii* LeConte (see ICZN, Third edition, Article 33[d]).

Taxa included in *Odontium:*
(for some synonyms, see Lindroth [1963], Erwin [1984], and Morita [1987])

B. bowditchii LeConte, 1878:451. (WY, ID, WA, BC) !
B. foraminosum Sturm, 1825:183. (Europe) !
B. striatum (Fabricius), 1792:179. (Palearctic) !
B. suturale Motschulsky, 1850:16 (Caucasus)
B. persimile Morawitz, 1862:225. (Japan, northeastern China) !
B. gebieni Netolitzky, 1928:168. (China)
B. japonicum Jedlička, 1961:311. (Japan)
B. soederbomi Jedlička, 1965b:203. (Mongolia)
B. robusticolle Hayward, 1897:50. (U.S.A.) !
B. coxendix Say, 1823a:151. (U.S.A., Canada) !
B. carinatum (LeConte), 1851:186. (CA, AZ) !
B. sculpturatum (Motschulsky), 1859:132. (CA, NV, WA) !
B. confusum Hayward, 1897:52. (U.S.A., Canada) !
B. arizonae Lindroth, 1962:246. (AZ, Mexico) !
B. durangoense Bates, 1891:263. (AZ, Mexico) !
B. aenulum Hayward, 1901:156. (IW, NK) !
B. sp. nr. *aenulum* (MS, MO) !
B. aeneipes Bates, 1883:276. (Japan, China) !
B. fusiforme Netolitzky, 1914b:168. (Formosa, Japan) !
B. subfusum Darlington, 1959:335. (Philippines) !
B. chloropus Bates, 1883:277. (Japan) !
B. suensoni Kirschenhofer, 1984:58. (Korea)

Subgenus *Bracteon* Bedel

Bembidion sensu LeConte, 1848, not Latreille, 1802.
Bracteon Bedel, 1879:27. (Type species *Bembidion litorale* [Olivier], designated by Bedel [1881].)
Chrysobracteon Netolitzky, 1914a:166. (Type species *Bembidion velox* [Linné], designated by Netolitzky [1940].)
Parabracteon Notman, 1929:157. (Type species *Bembidion tuberculatum* Notman [=*B. carinula* Chaudoir], by monotypy.)
Litoreobracteon Netolitzky, 1940:160. (Type species *Bembidion litorale* [Olivier], by original designation.)
Argyrobracteon Netolitzky, 1940:162. (Type species *Bembidion argenteolum* Ahrens, by original designation.)
Conicibracteon Netolitzky, 1940:162. (Type species *Bembidion stenoderum* Bates, by original designation.)
Stylobracteon Netolitzky, 1940:163. (Type species *Bembidion baikaloussuricum* Netolitzky [=*B. conicolle* Motschulsky], by original designation.)
Foveobracteon Netolitzky, 1940:164. (Type species *Bembidion foveum* Motschulsky, by original designation.)

Notes about synonymy

The name *Chrysobracteon* Netolitzky has traditionally been applied to this group, with the name *Bracteon* Bedel referring to *B. striatum* and its relatives (see, for example, Netolitzky, 1942 and Lindroth, 1963). However, as Bousquet and Larochelle (in press) note, the type species of *Bracteon* is *B. litorale* (as designated by Bedel [1881:xxiii]), not *B. striatum*. Thus, *Bracteon* must be applied to *B. litorale* and its relatives, with *B. striatum* falling within the subgenus *Odontium* LeConte.

Andrewes (1935), Lindroth (1963), Erwin and Kavanaugh (1981), and Erwin (1982) avoid use of subgeneric names, and use instead more informal species-group names for groupings within *Bembidion*. If this practice were followed for *Bracteon*, it could be referred to as the *B. inaequale*-group, as Lindroth (1962) did for the Nearctic fauna, or, perhaps more appropriately for the world fauna, the *B. litorale*-group.

Characterization of *Bracteon*

Adult Diagnostic Combination. Most easily recognized by possession of two "silver spots" on each elytron, that is, with a distinct patch of granulate microsculpture surrounding ed3 and ed5 (Figs. 5–23, 61). Most species have as well dark, shiny patches of weaker microsculpture on the elytral disc; these are termed "mirrors" (Figs. 7–23). Other character states as for *Odontium* subgeneric group.

Adult Description. **Size.** Relatively large *Bembidion*, SBL = 4.4–7.1 mm. **Color.** Body black or piceous, unspotted by pigment (although variation in microsculpture and metallic sheen produces a spotted pattern). Generally with metallic reflection (except in some black, presumably old and worn specimens), ranging in color from reddish, to coppery, golden, aeneous, green, blue-green, or bright blue. At least some parts of appendages paler, either testaceous, rufotestaceous, or rufous. **Microsculpture**. For the most part isodiametric on dorsal surface, although slightly transverse in some *B. hesperium* Casey. **Sensilla**. Basilateral seta of prothorax at hind angle. Setae ed3 and ed5 in third interval, not attached to stria; ed4 absent; eo1 generally far in front of eo2–eo4. Protarsomere 4 with ventroapical setae present, narrowly or widely separated. **Thorax**. Pronotum with tubercle between basilateral fovea and side margin. Elytral striae punctatostriate, including 8 and 9; striae 2 and 3 generally deepened and with larger punctures around silver spots (most extreme in *B. hesperium*); stria 8 more shallowly impressed anteriorly than 7, interval 8 relatively wide (Fig. 2). Elytral margin angulate at humerus; humeral margin reaching striae 4 to 6. **Male genitalia**. Internal sac with large dorsal plate; with central sclerite complex consisting of right and left lobes, both moderate to large, as well as a short to medium-length flagellum; with a ventral sclerite patch of two basins separated by a ridge (Fig. 99). Parameres with a varied number of setae, but generally trisetose (for example, of the 102 parameres of *B. lapponicum* studied, 62 had three apical setae, and 37 had four). **Female genitalia**. Spermatheca sclerotized, with a distinct ringed cornu; cornu without prominent apical indentation (Figs. 165–179). Spermathecal duct relatively short, with only a few turns and coils, not multiply coiled (Fig. 145). Sclerotized plate at base of spermathecal duct absent. Female basal stylomere (S1) setose (except in *B. carinula*, members of which have a few minute peg-like sensilla in place of setae). **Chromosomes**. Male 2n = 20+XY or 22+XY or 34+XY; chromosomes of normal size for *Bembidion* (autosomes 1.2–2.5 μm), submetacentric or metacentric (D. Maddison, 1985b:fig. 1; Nettman, 1986).

Larval Diagnostic Combination. Not yet distinguishable as a group from members of subgenera *Odontium* and *Ochthedromus;* the description below applies equally well to the known *Bracteon*, *Odontium*, and *Ochthedromus* larvae.

The larval instars can be distinguished by the following key:

1. Parietale with denticulate microsculpture near coronal suture (Figs. 226 to 231). Stipes with two setae on outer margin .... first instar
1′. Parietale with microsculpture near coronal suture consisting of shallow meshes or scales, not denticulate. Stipes with three setae on outer margin. Cervical groove prominent 2
2(1′). Head capsule narrower (LHw = 510–750 μm); stipes of maxilla relatively short and wide (length/width = 2.50–3.05) .... second instar
2′. Head capsule wider (LHw = 630–1040 μm); stipes of maxilla relatively long and thin (length/width = 3.22–3.89) .... third instar

First Instar Description. **Size**. LHw = 330–505 μm, LHl = 255–390 μm. **Color**. Frontale generally with one central dark spot, and one elongate dark patch on either side of the posterior portion of the frontale (Fig. 215); parietale in several species with dark patch on each side posteriorly near coronal suture (Fig. 215). Some species (*B. balli*, *B. foveum*) with these patches partly masked by generally dark ground color; others (*B. argenteolum*, *B. alaskense* Lindroth, *B. carinula*, and *B. lapponicum*) without distinct patches, having only diffusely darker head center or uniformly dark head. **Microsculpture**. Frontale without a row of a few large denticles; with or without a posterolateral patch of small denticles or multitoothed combs. Parietale with smooth patch mostly lacking microsculpture between FR$_4$, FR$_7$, FR$_8$ and the frontal suture (with a few denticles in *B. punctatostriatum*); generally with denticulate microsculpture laterally. **Head**. Head capsule constricted posteriorly; coronal suture short (LCl/LHl mean = 0.127, n = 11 species, 35 specimens).

Second Instar Description. As for *Bembidion*, plus: Stipes with three setae on outer margin.

Species included

Bracteon includes 17 known species, ranging throughout the temperate, cold-temperate, and subarctic regions of the northern hemisphere. Delimitation, identification, and description of these species are dealt with later, in the section "Species of *Bracteon*."

One Chilean *Bembidion* species, *B. chlorostictum* Reed (1874), was included in the subgenus by Csiki (1928). Reed (1874), Netolitzky (1931), and Lindroth (1962) considered the Chilean species to be unrelated to *Bracteon* as elytral interval 8 merges with 9 posteriorly as in subgenus *Notaphus* and related *Bembidion*, in contrast to the presumably primitively separated intervals 8 and 9 of *Bracteon*. However, *B. chlorostictum* shares with *Bracteon* "discoloured shining streaks on the third elytral interstice" (Reed, 1874); that is, shallowly microsculptured mirrors. Reichardt (1977) maintains *B. chlorostictum* within *Bracteon*, citing Jeannel (1962) as an authority for this action. As Perrault (1981:245) notes, Reichardt was in error in attributing to Jeannel (1962) the return of *B. chlorostictum* to *Bracteon*, as the species was not mentioned in Jeannel's work. Indeed, Jeannel (1962:536) states, "Quant aux séries phylétiques d'*Ocys*, de *Cillenus*, de *Bembidium*, d'*Odontium*, d'*Asaphidion* définies dans la Faune de France, elles n'ont aucun représentant dans l'hémisphère austral," indicating that he does not believe *Bracteon* (a taxon he includes within *Odontium*) occurs in South America. I could not locate type material of *B. chlorostictum*. D. H. Kavanaugh informs me (pers. comm., 1984) that no authentic *B. chlorostictum* specimens could be found in the Reed collection at the California Academy of Sciences. I have thus not seen specimens that I can definitely assign to *B. chlorostictum* Reed, nor to my knowledge has any recent carabidologist, but I suspect, as does Perrault (1981), that *B. chlorostictum* is related (if not identical) to *B. (Notaphiellus) cupreostriatum* Germain. I have examined two unidentified species of *Notaphiellus* (MCZ!), both from Chile. They possess distinct *mirror* patches around ed3 and ed5 (not silver spots); the elytra are a patchwork of mirrors and more deeply microsculptured areas. The male genitalia of the one specimen I studied is clearly "notaphoid," with a large, doubled, scaled ventral sclerite patch; the form of the internal sac structures is very similar to some North American *Notaphus* such as *B. graphicum* Casey. *B. chlorostictum* Reed is therefore probably also of notaphoid stock, and not a *Bracteon*.

Natural history

Bracteon are shoreline insects, spending most of their lives on vegetationless or sparsely vegetated beaches. In general, they occur on sandy substrates, which may or may not contain fine-grain silts and clays. This uniformity of broad habitat requirements allows rich *Bracteon* communities along some watercourses: I have found six species (*B. balli*, *B. foveum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, *B. levettei carrianum*) in company of related *B. coxendix* and *B. bifossulatum cheyennense* on the barren shores of the North Saskatchewan River near Paynton, Saskatchewan (Fig. 190), and occurrence of four or five species together is not uncommon (Lindroth, 1962; my observations). Most shores inhabited by *Bracteon* have at least two species. The means by which these ecologically and phylogenetically similar species coexist in an apparently uniform habitat is uncertain, but a closer examination of the animals and their habitats reveals a greater ecological diversity than is at first evident.

Lindroth (1945) and Andersen (1970) have shown that each European species prefers slightly different habitat substrates. On several beaches in North America, adults of different species were generally found in different microhabitats (my observations). Along the North Saskatchewan River near Paynton, for example, *B. foveum* is commonest around the clay-mixed banks of backwater pools (but many specimens are found along the river shore); *B. balli* and *B. lapponicum* on wet sand close to the river shore; *B. levettei carrianum* on wet sand along the river shore and backwater pool shores; *B. carinula* on sand, including the dry, wind-blown sand of the upper banks as well as along the river shore; *B. punctatostriatum* only on hot, dry sand more than 10 m from the river. These patterns appear to hold throughout the range of each species, but the North American species have not been studied in detail; my data are based on passing observations, lacking careful measurements. I have not collected most of the other species extensively enough to discover microhabitat preferences, but ranges of two other species are nonetheless quite clear: *B. inaequale* is found on clay-mixed sand, usually with a sparse cover of vegetation, around shores of creeks, rivers, and lakes; *B. zephyrum* is almost restricted to wind-blown sand beaches of the Pacific Ocean.

Behavioral observations of *Bracteon* are notably scarce. Andersen (1978) studied tunneling of several species, and showed that adults of *B. argenteolum* dig prodigiously into sand, *B. velox* and *B. lapponicum* extensively but to a lesser extent, and *B. litorale* rarely. Andersen (1978) also conducted substrate preference tests on *B. argenteolum*, *B. lapponicum*, and *B. litorale*, finding that *B. argenteolum* prefers finer dry sand to coarser dry sand, and *B. litorale* dry silt to dry sand. This is more or less consistent with the natural substrates of these beetles.

Bracteon adults are predacious: besides occasional reports of adults feeding upon various arthropods (Gersdorf, 1937; my observations), I have noted, in the course of dissecting numerous specimens of most *Bracteon* species, recta filled with pieces of arthropod cuticle. The full course of their diet is unknown.

Bracteon adults are generally active during the day, especially under bright summer sunshine, but they are at least occasionally nocturnal (against Larochelle, 1975). On the shores of the North Saskatchewan River at Deer Creek Bridge in Saskatchewan, a large number (123) of adults were collected between 21:30 and 22:30, 0.5 to 1.5 hours after sunset on a warm, moonless, September night. The adults were active on the surface, and several were feeding on dead insects, including nematocerous flies. A similar observation was made at the same locality on a cool, July night. That this is a general phenomenon has yet to be demonstrated.

Bracteon overwinter as adults, and breed in the late spring and early summer. There are three larval instars, and pupation presumably occurs in mid to late summer. Teneral adults appear in the late summer and fall.

I have observed adults of all eleven North American species in flight; among strictly Palearctic species, members of *B. argenteolum*, *B. velox*, and *B. litorale* have been observed flying (Lindroth, 1945). On warm, sunny days they are very active fliers, and will take to the wing quickly if approached, rather as do *Cicindela* adults.

Character states of *Bracteon*

Variation in many characters was seen within *Bracteon*. Some of this variety was useful in delimiting species, some for reconstructing phylogeny; some appeared useful for neither. In this section I introduce some of the character systems studied, describe some of the variation observed, and include tips for examination. I also comment briefly on characters that show potential for future research, but which I have only superficially examined. If, during the course of using this paper, some question arises concerning a character that cannot be answered by the cited figures or descriptions, this section should be consulted.

Color. The metallic hues of the body of *Bracteon* specimens as seen under diffuse light are relatively distinct, and need no introduction. I rarely use them in formulating my systematic conclusions, in good part because of the large amount of within-taxon variation. I include them for the value they have in aiding identification of some species.

Appendage color is less variable within species, but it can be more difficult to determine the color of an appendage as it would be in its pristine state, because of grease darkening the paler regions of the appendage. Specimens to be examined should be as clean as possible.

Microsculpture. The most striking features of the microsculpture of a *Bracteon* are silver spots on elytra of all species, and mirrors on elytra of some. These features are clearly studied under diffuse light on clean specimens.

Distinct silver spots are only found around discal setae ed3 and ed5 of the elytra, although indistinct silvery spots are present on the pronota of specimens of *B. inaequale* and some other related species. The number of silver spots, while generally two per elytron, varies to a considerable extent in some populations of *Bracteon*. For example, in a series of 94 specimens of *B. lapponicum* from Old Crow River, northern Yukon territory, Canada (DRMa, UASM), 36 (or 19.1%) of the 188 elytra had three setiferous silver spots; four had one silver spot, one had four silver spots, while the remaining 147 elytra had two silver spots.

The difference visible between silver spots, mirrors, and other portions is often due to differences in the metallic hue of these regions, in addition to the depth of the microsculpture lines. As well, silver spots are depressed within the elytra, and mirrors are generally raised, further enhancing the distinctiveness of each region. For example, the depressed silver spots of *B. zephyrum* are silvery-gray or blue-green, the raised mirrors generally dark coppery red or purplish, and the surrounding elytral surface has a green or blue-green reflection. On their own, the microsculpture differences are not always striking (see, for example, the scanning electron micrograph of Fig. 61). In some species, especially shiny *B. semenovi*, *B. punctatostriatum*, and *B. stenoderum*, the mirrors and silver spots are not nearly so distinctive, because of the general reduction of microsculpture on these animals. The extent of mirrors on these beetles can best be observed in the more deeply microsculptured females.

Some species (especially *B. argenteolum*, *B. alaskense*, *B. carinula*, and *B. punctatostriatum*) exhibit a great variation in overall microsculpture depth, with specimens ranging from shiny to dull. As a result, the absolute depth of microsculpture of mirrors and silver spots varies from specimen to specimen, so that some individuals may have shiny mirrors (or silver spots), while others have quite dull mirrors (or silver spots). Thus, mirrors and silver spots must be defined by *relative* microsculpture depth, not absolute depth; the pattern within an elytron of relative microsculpture depth is more or less constant within a species.

Some generally shiny specimens, lacking areas that would be deemed mirrors on the basis of markedly shallower microsculpture, nonetheless have central patches of a distinct metallic color in regions that would typically contain microsculpture mirrors. For example, while the shiny elytra of the *B. semenovi* holotype lack distinctly shinier patches, intervals 3 to 5 are darker, having a coppery tint lacking on the outer intervals; I consider this tint to delimit faint mirrors, homologous to the more distinct mirrors of other species.

The extent and distribution of mirrors provide some of the best characters for species delimitation and identification. When present, mirrors occur on interval 3, surrounding the silver spots. There may also be mirrors on intervals 1 through 5 near the center of the elytra, as well as on the anterior portions of the same intervals, or the posterior portions of intervals 6 and 7. In general, mirrors on intervals 3, 5, and

7 are more prominent than those on other intervals. Figures 7 to 23 illustrate some of the variation in mirror extent and position.

Sensilla. I investigated only a few adult sensillar characters, all setal.

One such character is suborbital setation. The head laterally beneath the eyes is either barren of setae (for example, in *B. punctatostriatum*, Fig. 60), or has a number of setae, ranging from relatively dense and long (*B. lapponicum* and others, Fig. 59), to shorter and sparser. The distinction between these states is not clear-cut, and as I have not quantified states, this character is relatively prone to errors in interpretation.

Protarsomere 4 of both sexes of most species of *Bembidion* possess ventrally an apical set of four setae, the two inner of which are thin, almost transparent, dorsoventrally flattened, and laterally expanded (Fig. 96a). The bases of these setae are generally close-set, almost touching in the midline. However, three *Bracteon* species have relatively cylindrical setae, with one of these species, *B. alaskense*, having their bases widely separated (Fig. 92).

Several sensillar characters showed variation within *Bembidion:* number of setae on the anterior margin of the labial palpomere 2; number of setae of submentum; tarsomere 5 setation; profemur setation; metafemur setation. These might provide evidence in future studies about *Bembidion* relationships.

Head. There is a wealth of mouthpart characters showing variation within *Bracteon*, but I have been able to examine only a few of them. Mandibles vary in overall shape, in microsculpture (especially of the terebral/premolar region [Figs. 32–34]), in distinctiveness of premolars (compare Figs. 32 and 33), and in size of pores dorsally and mesally near the dorsal condyle (Figs. 35–36). My preliminary study of these characters revealed extensive infraspecific variation within most of them, and I did not pursue them. Laciniae vary in width from narrow (Fig. 46) to robust and wide (Fig. 48). The shape varies in addition to simple width: some specimens have more definitely curved apices, or subapical indentations (Figs. 43, 44), or subapical ridges (Fig. 44); these characters warrant further study.

The shape of the mentum tooth has been used by Netolitzky (1942) and others as a character for *Bracteon* taxonomy. Netolitzky (1927,1942:33–34) cautions against overestimation of the value of the mentum tooth as a systematic character; however, he does use it to separate his "subgenera" *Litoreobracteon*, *Argyrobracteon*, etc. Lindroth (1962:1) disagrees with this use, claiming that the mentum tooth is too infraspecifically variable: "for instance, the two male paratypes of *carrianum* Csy. (=*levettei* Csy.), both from St. Albert, Alberta, and with identical penis, have a quite different mentum tooth, triangular in one, practically parallel-sided in the other specimen." While there is some variation in shape of the mentum tooth within *Bracteon* species, the variation I have seen is slight, and I consider it a stable enough character to be taxonomically useful. Even within *B. levettei* the mentum tooth is constant. I have examined the two paratypes of *B. carrianum* (USNM!) mentioned by Lindroth, and found them both to have the bulbous, parallel-sided mentum teeth characteristic of other members of *B. levettei*. Figures 49–56 illustrate some of mentum tooth shapes found in *Bracteon*.

Elytra. Two elytral characters not carefully studied herein but which should be investigated are: interval 3 width; anterior protrusion of humerus (protruding in *B. punctatostriatum*, *B. inaequale*, and to a lesser extent in some other taxa).

Metathoracic Wings. Two wing characters of potential future use are: pigmentation of metathoracic wing veins; shape of plica vein, whether sharply or gently curved.

Legs. Both sexes of many bembidiines and trechines have an apical projection bearing four setae ventrally on protarsomere 4; the length of this projection varies between species, and is essentially absent in *B. alaskense*, *B. argenteolum*, and *B. punctatostriatum*. Under a light microscope, however, the length of such a projection can be difficult to determine accurately. My observations of this structure therefore provide only uncertain evidence about relationship.

Claw shape, male protarsomere 1 and 2 shape, and protibial apices also show interspecific variation, but I have not studied these in great detail.

Male Genitalia. Because of the importance of male genitalia as a source of characters for species identification and phylogenetic analysis, I will describe their complicated structure in some detail.

Bracteon aedeagi at rest consist of a sclerotized outer tube and a membranous internal sac, containing several sclerites, folded in an inverted position within the tube (Fig. 99). The internal sac is attached to the tube dorsally near the apex, at the *ostium* (Lindroth, 1957b); this is the entrance into the internal sac from the exterior. During copulation the internal sac everts through the ostium; everted sacs are shown in Figures 101 to 103. I will first describe the internal sac as it sits in a rested, inverted position, beginning at the ostium. Many of the features are illustrated in Figures 99 to 102.

At the ostium the left and right external walls of the aedeagus extend inward. The ostial cavity formed by these two walls is bounded anteriorly where they join (Fig. 99, "anterior edge of ostial cavity"). The natures of the microtrichia and scales in the "ostial microtrichial patch" associated with this edge provide good characters for species identification. These microtrichia or scales occasionally extend upward, forming a *dorsal field* on the outer wall of the aedeagus. The walls of the ostial cavity are membranous anteriorly and posteriorly, but centrally they are sclerotized in a roughly triangular patch called the *ostial flag* (Lindroth, 1940).

A pathway into the internal sac is shown by the arrow in Figure 99. The ostial cavity ends ventrally as the two enclosing membranes fold together to the right and continue on the right side of the cavity upward to near the dorsal surface; anteriorly they extend upward to the *dorsal plate*. Nearer the ostium, they are folded again to the right, and extend back down toward the venter. This simple pattern is complicated in some species by additional folds or membranous lobes. Anteriorly, near the sclerite complexes, membrane structure is much more complex, and I have not yet resolved the folding pattern.

There are two sclerite complexes on the internal sac. The largest, and the one to which the sperm duct connects, is the *central sclerite complex* (CSC, Figs. 99–102). It is partly enclosed by the dorsal plate. The left lobe of the CSC consists of two closely adjacent domes, from the rightmost of which a flange is extended down and merged with the right lobe. The right lobe often has a bulge dorsally on its left side; as the ventral edge of this bulge is heavily sclerotized, a dark line or ridge is visible on the lobe in lateral view in some species. The lobe is often sculptured: *B. lapponicum* usually has triangular scales and longitudinal striations, *B. inaequale* has a rugose surface, whereas *B. balli* and *B. foveum* usually are quite smooth. However, there seems to be a great deal of intraspecific variation, and I have not used this character in my analysis. Similar variation is also seen in microsculpture present on the left CSC lobe.

Apically from these lobes a complicated grooved spike (*flagellum*) projects; it is species-specific in form (Figs. 99–102, 109, 110, 129–144). It is presumably the conductor of sperm, and may enter the spermathecal duct during copulation (Schuler, 1960). As the flagellum is partly surrounded by a scaly *flagellar sheath*, it can be very difficult to see in inverted position. The flagellar sheath is most prominent among *Bracteon* species in the *B. argenteolum*-subgroup, *B. stenoderum*, *B. hesperium*, *B. lorquinii*, and the *B. inaequale*-subgroup. In Figures 112 to 128, I have emphasized the flagellum beyond its normal visibility, and I present in Figures 129 to 144 drawings of isolated CSCs including flagella. The flagella provide excellent characters for species identification in *Bracteon* and other *Bembidion;* if all other identification aids fail, I recommend dissecting out a CSC and comparing the isolated flagellum with Figures 129 to 144.

From the baso-dorsal portion of the flagellum a heavily sclerotized wrinkled structure (Lindroth's "*ribbon brush,*" "*brush sclerite,*" or "BW") arises and passes on the right side of the CSC down toward the venter, where it joins the *ventral sclerite patch* (VSP). This latter complex is quite varied within the subgenus, and is one of the most useful genitalic features for specimen identification. In *Bracteon*, it consists of two basins, connected by a dorsal ridge; the posterior basin extends distally into a wrinkled sclerotized patch.

Everted internal sacs clearly show lobes and surface sculpture of the membrane. SEM views of the membranes reveal a surprising complexity and diversity of microsculpture, with striking within-specimen (Figs. 103–106) and between species variation. I have not had time to study lobes or microsculpture in detail, but they seem to me to be some of the most, if not the most, fruitful areas for future *Bembidion* studies.

Female Genitalia. Female genitalia vary considerably from species to species, as well as within species. Some characters, such as length of stylomere 2, were seen to be fairly constant within most species. Many other characters, such as the number of dorsolateral ensiform setae, show more variation within species. Most aspects of spermathecal shape are quite varied within some species, but there are consistent differences between them. I figure the spermatheca of most species (Figs. 165–179), as some useful information is contained therein. Spermathecal shape should prove more useful in other subgenera and for studies of subgeneric delimitation and relationships.

Characters that have interesting patterns of variation, and which might prove useful in future research, include the form of sternum VIII, shape and setation of the valvifers (sternum IX), spermathecal duct coiling and turn pattern, and stylomere 1 structure. I have also not studied bursa copulatrix shape, although Erwin and Kavanaugh (1981) found it useful in their work on the *B. erasum* group.

Chromosomes. Chromosomes of all North American taxa of *Bracteon* have been investigated, as well as the Palearctic *B. litorale* (Nettman, 1986). Members of *Bracteon* are relatively constant in chromosome number, although there is some variation. Autosomes differ little in length. The only striking variation in form is found in Y chromosomes: all species have a Y equal in size to the autosomes, or only slightly smaller, except *B. alaskense* and *B. carinula*, which have Y chromosomes less than two-thirds the length of the smallest autosomes. Karyotypes and other details of these species' chromosomes, as well as localities of capture of specimens examined, are presented elsewhere (D. Maddison, 1985b).

Larva. The most obvious differences between first instar larvae of *Bracteon* species are in color, especially of the head. Closer examination, however, reveals numerous other differences, mostly in sculpture and setation. This observation matches that of Goulet (1983) on elaphrine larvae, on which he found many systematically useful microsculptural and sensillar characters. In *Bracteon*, variation among species was noted in microsculpture of the frontale, parietale, mandibles, and pronotum of first instars. The presence, length, and form of setae of the head capsule, thoracic nota, abdominal terga, and abdominal sternum IX also provided useful characters. For identification purposes, setal width and length are best characterized by comparison to nearby setae; thus I do not give absolute measurements. For example, I state that seta FR_3 of most *Bracteon* is basally less than one-third the width of the nearby FR_2, but the absolute basal widths have not been measured.

One of the few microsculptural characters I have investigated is frontal microsculpture. Most *Bracteon* have a patch of microsculpture posteriorly and laterally on the frontale, in the position of the postero-lateral dark spots on Figure 215. Descriptions of type of frontal microsculpture (whether or not multitoothed combs are present; character 64 of Table 2) are restricted to the anterior half of this patch, and characterization of extent of frontal microsculpture (character 63) applies only to the posterior half of the patch.

I have not carefully studied nasale structure; while there is much infraspecific variation, in good part due to wear, there are some differences between species. Urogomphus length varies between species, and is also worth further examination.

SPECIES OF *BRACTEON*

Species and Subspecies Recognition

Species concepts

The diversity of opinion about the meaning of "species" has lead to a voluminous literature. The definition one chooses to adopt, is, for the most part, dependent on what one wants to do with the resulting taxa. Different biologists may choose to divide organisms into species in different ways, each choosing a definition that is best suited for their fields. As a phylogeneticist, I adopt a species concept similar to that of the evolutionary species concept of Simpson (1961:153) and Wiley (1978, 1981), basically a rephrasing in phylogenetic terms of the Biological Species Concept (Mayr, 1940; Dobzhansky, 1937; Coyne, Orr, and Futuyma, 1988).

If we are to explain the origin of diversity of form, then we must use the "vehicles" of evolution (lineages) in our theories, if our theories are to be both explanatory and simple. For dioecious organisms, a species, as I use the term, is a portion of a lineage of a phylogeny, with a lineage being (somewhat vaguely) defined as a set of organisms cohesively linked by breeding ties, which is distinct from other such sets. In the genealogical nexus of organisms, the boundaries of species occur where the anastomizing lines within species are replaced by the gaps between lineages.

In dealing with fossils, the starting and the ending points of this portion are not easily decided. However, as the fossil record of *Bracteon* is inadequate, consisting of only a few Miocene and Pleistocene fragments, this is not a concern. To use a phrase from R. C. Fox, my specimens come from the "thin veneer of the present." Among Recent organisms a species consists of a time-transect of a lineage.

Lineages (and thus species as I use the term) are genealogical, and therefore some of the same sorts of evidence can be used for delimiting them as for subsequent inferences regarding their interrelationships, but here the pattern being sought is not simply one of sets of dichotomizing lineages, but also of anastomozing lines. We might detect anastomosing lines by at least two methods: by detecting discordant apomorphies indicating past joining of two once-independent lines (Wanntorp, 1983; Nelson, 1983), or by more-direct evidence of reproductive cohesion. Within one small monophyletic group, one kind of "more-direct evidence" might be repeated discovery of one form of male microsympatrically with just one form of female, in addition to some observed matings between the types. Similarly, we can detect lack of anastomosis between two forms by maintenance of distinctiveness in the face of sympatry. If in the area of sympatry there is a lack of the phenotypes expected if there were gene flow between the forms, then gene flow is probably absent or minimal, and the forms are maintaining their genealogical distinction.

Using morphological and geographic data, the boundaries of a species can be inferred by observation of a set of individual organisms possessing a unique combination of (ancestral or derived) character states. The character states might be structural, behavioral, or ecologic. Additional evidence may be provided in the form of directly observed matings between members of the set, or distinctiveness of sympatric forms. If the forms are allopatric or parapatric, the evidence may not be as clear. While no gene flow may be present at this exact moment between currently allopatric forms, the forms may have been genealogically connected very recently. Morphological distinctiveness is used as the clue: if two allopatric forms differ as much as two sympatric forms, they are judged to be long-established lineages and separate species; otherwise they are treated as subspecies.

Species delimitation within *Bracteon*

I will not present in detail my reasoning for my recognition of each of 17 species within *Bracteon*. Any two forms each with their own unique character combination, occuring sympatrically, are judged to be separate species. Suffice it to say that 17 forms maintain their distinctiveness where they occur sympatrically (Table 1). Geographically separated forms that show intermediate regions of intermediate specimens are considered as belonging to one species (eastern and western forms of *B. inaequale* are the clearest examples of this). Other parapatric or allopatric forms are judged on the basis of similarity. If the forms are very similar, only consistently differing in one or a few characters, I have recognized them as belonging to the same species (for example, *B. levettei levettei* and *B. levettei carrianum* Casey, the Lake Baikal and Alaskan *B. alaskense*, southern Nearctic and northern *B. lapponicum*). If, however, the forms differ by at least the same magnitude as do sympatric species, they are construed as distinct species (for example, *B. litorale* and *B. levettei*, *B. velox* and *B. carinula*). This judgement is admittedly rather subjective; if any errors have been made, they are probably more errors in lumping than errors in splitting.

The phylogenetic analysis (presented later in the chapter "Phylogeny of *Bracteon*") indicated the monophyly of 10 of the 17 *Bracteon* species: *B. foveum*, *B. alaskense*, *B. semenovi*, *B. stenoderum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, *B. hesperium*, *B. zephyrum*, and *B. inaequale;* the phylesis of the other seven species was not apparent. Note, however, that paraphyly or polyphyly of most species could not be detected by the methods I used (in order to do that, I would have needed to treat each specimen individually, an impractical task!).

One form which may be shown to be paraphyletic is *B. levettei;* I could not demonstrate that *B. levettei levettei* plus *B. levettei carrianum* constitute a monophyletic group. If future work shows *B. levettei* to be paraphyletic, and collections from the Alberta foothills indicate a lack of recent gene flow between the montane *B. levettei levettei* and the lowland *B. levettei carrianum*, then I would favor splitting of the taxon into two separate species. However, in the face of ignorance, I prefer to be conservative, following Lindroth (1963) in retaining montane and lowland specimens within one species.

Subspecies concepts

A subspecies is a phenetically distinct and geographically cohesive portion of a species, that is not connected to other such units by extensive geographic clines (such clines, if they do exist, are short and steep). Subspecies are units of convenience, recognized because they are worthy of discussion in comparative work. I recognize subspecies in only one *Bracteon* (*B. levettei*), although further work may reveal the value of similarly dividing at least *B. alaskense*, *B. lapponicum*, and *B. inaequale*.

Checklist of extant *Bracteon* taxa

B. balli Lindroth
B. foveum Motschulsky
B. argenteolum Ahrens
B. alaskense Lindroth
B. semenovi Lindroth
B. stenoderum Bates
B. carinula Chaudoir
B. velox (Linné)
B. lapponicum Zetterstedt
B. punctatostriatum Say
B. hesperium Casey

B. lorquinii Chaudoir
B. zephyrum Fall
B. levettei Casey
  B. levettei levettei Casey
  B. levettei carrianum Casey
B. inaequale Say
B. litorale (Olivier)
B. conicolle Motschulsky

KEY TO ADULTS OF *BRACTEON*

To identify specimens of adult *Bracteon*, the key below should be consulted, as well as additional information provided in the account of each species. The figures (especially of habitus [Figs. 5–23] and male genitalia [Figs. 112–128]) may prove especially helpful.

1. Distinct smooth patches ("mirrors") on elytra, at least on interval 3 surrounding silver spots, or elytra generally smooth and shiny (Figs. 7–23) 3

1′. Distinct elytral mirrors lacking, interval 3 between silver spots dull (Figs. 5, 6) 2

2(1′). Pronotum small in comparison to the long elytra (El/Pwm = 2.44–2.60). Male protarsomere 1 relatively large (Fig. 76) .... *B. foveum* Motschulsky

2′. Pronotum and elytra of typical proportions (El/Pwm = 2.25–2.35). Male protarsomere 1 of normal size (Fig. 75) .... *B. balli* Lindroth

3(1). Intervals 6 or 7 with mirrors as or nearly as distinct as interval 3 mirrors, at or near level of silver spots (Figs. 17–23) 13

3′. Outer elytral intervals lacking distinct mirrors, more or less uniform in luster 4

4(3′). Midlateral seta of pronotum present (if the seta has broken off accidently, then its former presence is indicated by a pore puncture in the lateral margin) 5

4′. Midlateral seta of pronotum absent 8

5(4). Large (SBL generally more than 6.2 mm) and shiny, with wide body (Fig. 11). Prothorax wide at base, with sides little sinuate. Mentum tooth large, bulbous, rectangular, without distinct epilobes (Fig. 52) .... *B. punctatostriatum* Say

5′. Smaller (SBL generally less than 6.2 mm) and in most specimens duller. Body proportions more normal, not atypically wide (Figs. 12–14). Prothorax more constricted near base. Mentum tooth smaller, flatter, triangular or trapezoidal, epilobes distinct (Fig. 7) 6

6(5′). Pronotum with distinct, long carina inside hind angles near base; carina extended to basal edge of pronotum (Figs. 12, 70) .... *B. carinula* Chaudoir

6′. Basilateral carina, if present, thin, oblique, and short, not extended to basal edge of pronotum 7

7(6′). Third elytral interval wide, 1.7–2.6 times as wide as second. Pronotum flatter, with flaring hind angles. (Holarctic.) .... *B. lapponicum* Zetterstedt

7′. Third elytral interval narrower, 1.4–1.6 times as wide as second. Pronotum more convex, hind angles less prominent. (Palearctic.) .... *B. velox* (Linné)

8(4′). Small (SBL = 4.4–5.4 mm) specimen, elytra narrowing apically, striae deeply impressed; legs mostly pale, rufous. Generally with two setae in neighborhood of ed7. (Japan and neighboring mainland.) .. *B. stenoderum* Bates

8′. Generally larger, with wider elytra and less fusiform shape. Generally with one seta at ed7 9

9(8′). Shoulder margin longer (as in Figs. 68, 70, 71), reaching or nearly reaching stria 5. Aedeagi as in Figures 114 and 115; female S2s exceptionally long (Figs. 150, 151). (Palearctic region and Alaska.) 10

9′. Shoulder margin shorter (as in Fig. 69), reaching at most just beyond stria 6. Aedeagi as in Figures 121 and 122; female S2s of normal length (Figs. 157, 158). (Western North America south of Alaska.) 12

10(9). Legs pale rufous. Dorsal surface of body shiny, with inconspicuous mirrors and silver spots. Interval 3 narrow (Fig. 9) .... *B. semenovi* Lindroth

10′. Legs darker, at least apex of femur as well as tibia and tarsus infuscated. Duller, with mirrors and silver spots in most specimens more distinct. Interval 3 wider (Figs. 7, 8) 11

11(10′). Duller, elytra in most specimens distinctly duller than pronotum. ed3 and ed5 near center of silver spots. Extra setae between eo4 and eo5 generally absent. Protarsomere 4 ventroapical setae widely separated (Fig. 92) .... *B. alaskense* Lindroth

11′. Dorsal surface, including elytra, shinier. ed3 and ed5 at or near anterior edge of silver spots. Extra setae between eo4 and eo5 generally present. Protarsomere 4 ventroapical setae narrowly separated (Fig. 93) .... *B. argenteolum* Ahrens

12(9′). Small (SBL = 4.7–5.8 mm). Very shiny and dark. Microsculpture in shinier areas of elytral disc consisting of transversely stretched sculpticells, at least in males. Femora generally with basal half rufous *B. hesperium* Casey

12′. Larger (SBL = 5.3–6.8 mm). Duller and brighter. Elytral microsculpture isodiametric throughout. Femora entirely piceous or black *B. lorquinii* Chaudoir

13(3). Mentum tooth rectangular, bulbous, epilobes indistinct. (Nearctic.) 14

13′. Mentum tooth flatter, not bulbous, epilobes distinct 15

14(13). Mirrors on intervals 6 and 7 more or less isolated from mirrors on inner intervals, and present near level of posterior silver spot (Figs. 22, 23) *B. inaequale* Say

14′. Outer elytral mirrors broadly connected to inner mirrors; outer mirrors closer to anterior silver spots. (Figs. 20, 21) *B. levettei* Casey

15(13′). Lateral margins of pronotum wide, flared into protrudent front angles (Fig. 19). (Pacific coastal beaches of North America.) *B. zephyrum* Fall

15′. Pronotal margins narrower (Figs. 17, 18). (Palearctic.) 16

16(15′). Pronotum flatter with sides at most slightly sinuate; midlateral seta absent; ed3 and ed5 generally at anterior edge of silver spots *B. conicolle* Motschulsky

16′. Pronotum more convex, sides more rounded; midlateral seta present or absent; ed3 and ed5 generally closer to center of silver spots *B. litorale* (Olivier)

KEY TO FIRST INSTAR LARVAE OF THE *ODONTIUM* SUBGENERIC-GROUP

In the following key I have included first instar larvae of all eleven North American *Bracteon* species; I have omitted *B. argenteolum* and *B. litorale*, the larvae of which were described by Andersen (1966), as I have not seen specimens. I have also incorporated all other known larvae of the *Odontium* subgeneric-group, as these cannot yet be separated as a group from those of *Bracteon*.

1. Parietale each with 2–6 large, tooth-like egg bursters in a cluster on each side near coronal suture (Figs. 228, 234); setae PR$_{13}$, ME$_{14}$, TE$_{11}$ short (Fig. 250) *B. carinula* Chaudoir

1′. Parietale each with more numerous, smaller denticles (Figs. 226–227, 229–233, 235); if egg bursters large, then not set in a small cluster; setae PR$_{13}$, ME$_{14}$, TE$_{11}$ relatively long (Figs. 240, 248) 2

2(1′). Setae ME$_2$ and TE$_6$ small (Figs. 246, 254) 3

2′. Setae ME$_2$ and TE$_6$ relatively long (Figs. 245, 252) 5

3(2). Head capsule dark; pronotum with faint traces of microsculpture; seta PR$_{10}$ present and long *B. lapponicum* Zetterstedt

3′. Head capsule pale with five dark spots; pronotum with distinct microtubercles; PR$_{10}$ absent or small 4

4(3′). Seta EP$_1$ of abdominal segments 2–6 long, greater than one-third the length of EP$_2$; FR$_3$ thin, less than one-third the width of FR$_2$; PR$_{10}$ present, short; setal groups gPR and gME absent; TE$_\alpha$ absent; pronotum with microsculpture lacking between the two PR$_{14}$s *B. (Ochthedromus) bifossulatum cheyennense* Casey

4′. Seta EP$_1$ very short, less than one-fifth length of EP$_2$; FR$_3$ thick, basally greater than one-half width of FR$_2$; PR$_{10}$ absent, replaced by setal group gPR; gME and TE$_\alpha$ present; pronotum with microsculpture present between the PR$_{14}$s *B. punctatostriatum* Say

5(2′). Small (head capsule width 275 μm); head only slightly constricted posteriorly (Fig. 223), with long coronal suture (LCl/LHl = 0.196); frontale lacking microsculpture, with faint midlateral dark spots; parietale with large, widely separated egg bursters *B. (Odontium) aenulum* Hayward

5′. Larger (head capsule width 330 μm or more); head more definitely constricted posteriorly (Figs. 210–217, 219, 220), with shorter coronal suture (LCl/LHl < 0.165); frontale generally with posterior-lateral microsculpture (lacking only in *B. alaskense*), with or without dark spots; parietale with smaller denticles 6

6(5′). Frontale lacking microsculpture posteriorly, parietal microsculpture consisting of long, thin denticles (Figs. 227, 233); head capsule wide (LHw > 490 μm, LHw/LHl = 1.35–1.47) *B. alaskense* Lindroth

6′. Frontale with multipointed or singly pointed microsculpture, parietale with smaller denticles (Figs. 226, 231, 232); head capsule narrow (LHw < 470 μm, generally < 420 μm, LHw/LHl = 0.99–1.37) 7

7(6′). Head capsule more or less uniformly dark 8

7′. Head capsule mostly pale, or pale with three dark spots upon the frontale and generally one on each parietal side 9

8(7). Seta TE$_{11}$ thin, blunt, parallel-sided; much narrower than TE$_{10}$ ...... *B. foveum* Motschulsky
8′. Seta TE$_{11}$ tapered, about as thick basally as TE$_{10}$ ...... *B. balli* Lindroth
9(7′). Anterior two-thirds of posterior-lateral microsculpture patch of frontale consisting of relatively large, single denticles; nasale blunt (Fig. 193) 10
9′. Posterior-lateral microsculpture mostly multitoothed combs; where single denticles, these are relatively small; nasale generally more sharply pointed (Fig. 192) 11
10(9). Microsculpture of parietale near coronal suture absent or very sparse ...... *B. hesperium* Casey
10′. Microsculpture of parietale near coronal suture more extensive and prominent ...... *B. lorquinii* Chaudoir + *B. inaequale*-subgroup
11(9′). Pronotum with microsculpture (small tubercles) between PR$_8$, PR$_9$, and PR$_{10}$ 12
11′. Pronotum lacking microsculpture ...... *B. (Odontium) bowditchii* LeConte + *B. (O.) foraminosum* Sturm
12(11). Mandible long, markedly curved (Fig. 200) ...... *B. (Odontium) coxendix* Say
12′. Mandible shorter, less curved (similar to mandible of Fig. 199) ...... *B. (Odontium) confusum* Hayward

Accounts of Species of *Bracteon*

The arrangement of *Bracteon* below matches that of the inferred phylogeny of the group, presented in the section "Phylogeny of *Bracteon*." I include within *Bracteon* two subgroups, the *B. argenteolum*-subgroup and the *B. inaequale*-subgroup, together containing seven of the 17 species. The *B. argenteolum*-subgroup contains *B. argenteolum*, *B. alaskense*, and *B. semenovi;* see the section "Comparison with related species" under *B. argenteolum* for a discussion of this subgroup. The *B. inaequale*-subgroup, defined by extensive elytral mirrors, straight CSC flagella, 10 pairs of autosomal chromosomes, and similar larvae, includes *B. levettei*, *B. inaequale*, *B. litorale*, and *B. conicolle*. The other ten species are not arranged in subgroups.

Bembidion balli Lindroth

Bembidion balli Lindroth, 1962:15. HOLOTYPE male examined, in CNC, labeled: "McMurray, Alta. VIII.11.53 George E. Ball / Holotypus balli Lth. [red label, in Lindroth's handwriting] / HOLOTYPE CNC No 8375 [red label]." Type locality Fort McMurray, Alberta.

Derivation of Specific Epithet. Patronym given by C. H. Lindroth to honor his friend and fellow carabidologist, George E. Ball.

Characteristics of Adult. (Figs. 5, 35, 40, 49, 62, 68, 75, 96, 98, 99–102, 109, 112, 129, 147, 148, 165, 184, 186.)

Diagnostic combination. Body proportions as in Figure 5; distinct elytral mirrors lacking; pronotum lacking long basilateral carina; male protarsomere 1 of normal size (Fig. 75); male aedeagus with flagellum long and ventrally curved (Fig. 129), apical boundaries of the two basins of the VSP well separated in left lateral view (Fig. 112).

Comparisons with related species. Difficult to distinguish from specimens of *B. foveum*. *B. balli* members are smaller, with broader prothoraces and shorter, more convex elytra (compare Fig. 5 of *B. balli* with Fig. 6 of *B. foveum*). For *B. balli*, El/PWm = 2.25–2.35 (n = 7); for *B. foveum*, El/PWm = 2.44–2.60 (n = 9). *B. balli* generally more golden in color. Microsculpture of most specimens more deeply engraved, surface therefore duller, especially on forebody; microsculpture around anterior discal seta of elytron (ed3) irregularly disrupted in most specimens (Fig. 62), as opposed to the more smoothly circular pit in *B. foveum* (Fig. 63). In *B. foveum*, an extra seta is generally present on the elytra between eo4 and eo5, lacking in *B. balli*. Pores on surface of mandibles just mesal of dorsal condyle (Fig. 35) much narrower than those of *B. foveum* (Fig. 36); confirmed in four specimens of each species. As well, front angles of pronotum somewhat less protruded in *B. balli*, and humeral margin generally longer and more angulate. Males of *B. balli* can be distinguished by the considerably smaller basal protarsomeres (Fig. 75). Most external characters require experience to interpret, and, until this is gained, I recommend examination of the male aedeagus for more certain identification. Aedeagus thinner, less curved than in *B. foveum*, with narrower apex; right lobe of CSC generally less protruded in *B. balli;* apical boundaries of the two basins of the ventral sclerite patch of *B. balli* more widely separated in left lateral view; flagellum much longer, thinner, more curved in *B. balli.*

B. balli are occasionally confused with dark, unmetallic specimens of *B. carinula* lacking distinct mirrors (apparently through wear); however, *B. balli* adults do not have a long basilateral carina confluent with the pronotal base.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.8–5.8 mm. Dorsal surface bronze or gray-bronze, silver spots blue, bronze, or aeneous. Appendages for the most part piceous, except for the venter of antennomere 1, the pro- and mesotrochanters, and the base and venters of femora, which are testaceous; antennomeres 2 through 4 and tibiae paler ventrally in some specimens. Silver spots inconspicuous, not or only slightly depressed below rest of interval; elytra lacking mirrors, although interval 3 in some specimens slightly darker between silver spots, giving the illusion of very faint mirrors. Sides of pronotum sinuate, greatest width at or slightly before middle. Elytral striae slightly to moderately impressed; interval 3 not or only slightly wider than 2. Spermatheca as in Figure 165, ramus lobe in many specimens longer; cornus long, slightly curved, dorso-basal bulb curved, short. No posterior lobe at base of spermathecal duct. Stylomeres as in Figure 148.

Characteristics of First Instar Larva. (Figs. 191, 196, 210, 240, 242, 245, 248, 252, 255, 257.)

Diagnostic combination. Head capsule dark (Fig. 210), with faint trace of three-spotted frontal pattern; parietale with slightly darker patch in front of PA_4 and PA_7; parietal denticles small; ME_2 and TE_6 long; TE_{11} tapered, basally thick, as thick as TE_{10} (Fig. 248); abdominal segment VIII with EP_1 less than one-half width of EP_2.

Comparisons with related species. From the very similar *B. foveum*, distinguished by thick, tapered setae TE_{11} of the abdominal terga. As well, mandible of *B. balli* with only one or two denticles near seta MN_1, in contrast to the more numerous denticles of *B. foveum;* setae FR_1 and FR_3 shorter than those of *B. foveum.*

From the other *Bembidion* with dark larval head capsules, *B. lapponicum,* distinguished by many traits, including the smaller parietal denticles; narrow setae FR_1, FR_3, and segment VIII EP_1; long setae ME_2 and TE_6; absence of setae ST_2 on abdominal sternum IX.

Description. See Table 2 for character states. Additional traits follow. LHw = 400–415 μm, LHl = 360–380 μm, LCl/LHl = 0.132–0.147. Four specimens measured.

Characteristics of Second Instar Larva. (Fig. 258.)

Description. LHw = 540–595 μm (n = 2). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens Examined. I have seen 259 adults, 29 first instars, and 5 second instars from the following collections: AMNH, BMNH, CAS, CNC, CUIC, DRMa, HNHM, ICCM, MCZ, SMNH, UASM, USNM, ZIL, ZMLS.

Geographic Distribution. Found only in west-central Saskatchewan and at the type locality of Fort McMurray, Alberta (Fig. 261). The report of *B. balli* from Churchill, Manitoba (Elias, 1984), is based on a series of *B. carinula* adults (SAEl!).

Geographic Variation. None noted over the small known range.

Habitat. Known only from rivers, on barren beaches composed mainly of sand.

Phylogenetic Relationships. I place *B. balli* as the sister group of *B. foveum* (Figs. 292, 293).

Bembidion foveum Motschulsky

Bembidium foveum Motschulsky, 1845:271. LECTOTYPE male, designated by Lafer (1975), in ZMUM, not seen. Type locality L. Baikal, Russia.

Bembidion bryanti Carr, 1932:191 (not *B. bryanti* Andrewes, 1921:249). HOLOTYPE male examined, in CNC, labeled: "Norman, N.W.T. Sept.23.1929 Owen Bryant / Mackenzie River 1929 Trip. Lot Owen Bryant 23 / above San Sault Rapids 70 mi Norman [handwritten] / HOLOTYPE Bembidion bryanti Carr No 3435 [red label] / Holotype Bembidion bryanti Carr ex coll. F. S. Carr [red label] / SLIDE No. 2102 [green label] / Bembidion foveum Mtsch Det. Lindroth, 1961." Type locality Mackenzie River, 70 miles below Fort Norman, above Sans Sault Rapids.

Bembidion beringi Netolitzky, 1940:164. HOLOTYPE male examined by Lindroth (1962), in Swedish Riksmuseum, Stockholm. Type locality Petropavlovsk, Kamchatka, Russia.

Bembidion grahami Hatch, 1951:114. HOLOTYPE male examined, in OSUO, labeled: "Findlay Forks B.C. 22/6 1930 Coll. R. Graham [partly handwritten] / Bembidion (Chrysobracteon) foveum Mots. M. Hatch 1969 / bryanti Carr (Prob = Siberian species) Det. Lindroth, 1958 / TYPE Bembidion (Chrysobracteon) grahami 1950 - M. Hatch [red label, handwritten]." Type locality Findlay Forks, British Columbia, Canada.

Derivation of Specific Epithet. From the Latin *fovea*, meaning "pit," referring to the elytral silver spots.

Characteristics of Adult. (Figs. 6, 24–27, 29–32, 36, 37–39, 41, 63, 69, 76, 113, 130, 149, 166, 183.)

Diagnostic combination. Body proportions as in Figure 6; distinct elytral mirrors lacking; pronotum lacking long basilateral carina, with midlateral seta; male protarsomere 1 exceptionally large (Fig. 76); flagellum of male aedeagus relatively short and thick (Fig. 130); apical boundaries of two basins of VSP narrowly separated in left lateral view (Fig. 113).

Comparisons with related species. Similar to *B. balli;* many specimens difficult to identify with certainty using external characters. For a discussion of differences between the species, see account of *B. balli.*

Description. See Table 2 for character states. Additional traits follow. SBL = 5.5–6.5 mm. Dorsal surface grayish, in many specimens with bronze or aeneous tint; silver spots bronze, greenish, or bluish. Appendages colored as in *B. balli* but slightly darker, pale areas a bit more rufous. Disc of pronotum diffusely shinier. Elytral mirrors absent, although in some specimens the inner intervals are slightly shinier; silver spots in many specimens slightly more depressed into elytra than in *B. balli*. Sides of pronotum sinuate; greatest width generally further forward than in *B. balli*, before middle. Elytral striae shallow to moderately impressed; interval 3 only slightly wider than 2. Spermatheca as in Figure 166, similar to that of *B. balli*. No posterior lobe at base of spermathecal duct. Stylomeres as in Figure 149.

Characteristics of First Instar Larva. (Figs. 199, 201–203, 205, 211, 226, 232, 238, 249.)

Diagnostic combination. Head capsule dark, with faint trace of three-spotted frontal pattern; parietal denticles small; ME_2 and TE_6 long; TE_{11} parallel-sided, bluntly tipped, basally thin, less than one-half width of TE_{10} (Fig. 249); abdominal segment VIII with EP_1 less than one-half width of EP_2.

Comparisons with related species. Very similar to larva of *B. balli;* best distinguished by the thin, blunt, parallel-sided setae TE_{11} of the abdominal terga; a few more characters are mentioned under the account of *B. balli.*

From *B. lapponicum*, distinguished by the smaller parietal denticles; narrow setae FR_1, FR_3, TE_{11}, and segment VIII EP_1; long setae ME_2 and TE_6; absence of setae ST_2 on abdominal sternum IX.

Description. See Table 2 for character states. Additional traits follow. LHw = 460–465 μm, LHl = 410–415 μm, LCl/LHl = 0.135–0.146. Two specimens measured.

Specimens Examined. I have seen 645 adults and 17 first instars from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, HNHM, ICCM, JKLi, MCZ, OSUO, ROM, SMNH, UASM, UBC, UMHF, USNM, ZMLS.

Geographic Distribution. A Holarctic species (Fig. 262). In the Palearctic, from northeasternmost Europe, across the width of northern Asia to Kamtchatka. In North America (Fig. 262b), from Alaska east to Churchill, Manitoba, and south to central Saskatchewan.

Geographic Variation. No variation correlated with geography was noted.

Habitat. Found only on the banks of rivers, most commonly on barren, silt-mixed sand.

Phylogenetic Relationships. Apparently the sister species of *B. balli* (Figs. 292, 293).

Bembidion argenteolum Ahrens

Bembidion Argenteolum Ahrens, 1812:23. TYPE material lost (see Lindroth, 1962:11). Type locality Halle, Germany.

Bembidium azureum Gebler, 1833:276.

Bembidium chalybaeum Sturm, 1843:36. *Nomen nudum.*

Bembicidium glabriusculum Motschulsky, 1845:272. Holotype male examined, in ZMUM, labelled: "Sitka [red label] / Bembidium glabriusculum Mihi, Sitka [handwritten on bordered paper] / [blank red rectangular label]." Type locality apparently Sitka, Alaska (presumably incorrect, as no other specimens of this species has been taken from the New World).

(*Bembidion argenteolum* v. *amethystinum* Meier, 1899:98. [Name unavailable as clearly intended to be infrasubspecific.])

Bembidion argenteolum var. *virens* Schilsky, 1908: 604 (not Gyllenhal, 1827:407). Types presumably in the Schilsky collection, Zool. Mus., Berlin (Horn and Kahle, 1937). Type locality Posen (=Poznan), Poland. (Original description gives no indication that author intended the name to be infrasubspecific, and thus the name is available [ICZN, Third edition, Article 45(g)].)

Derivation of Specific Epithet. From the Latin *argentum*, meaning silver, referring to the sparkling, metallic appearance of the elytral "silver spots."

Characteristics of Adult. (Figs. 7, 77, 88, 93, 97, 114, 131, 150, 167.)

Diagnostic combination. Large (SBL = 5.4–7.0 mm, generally over 5.8 mm); elytral mirrors on intervals 3 and 5, in some specimens on first five intervals, no distinct mirrors on intervals 6 or 7; pronotum lacking long basilateral carina, without midlateral seta; ventroapical setae of protarsomere 4 narrowly separated (Fig. 93); lateral projection on male protarsomere 3 lacking (Fig. 93).

Comparisons with related species. Adults are very similar to those of *B. alaskense* and *B. semenovi*. Larger than *B. alaskense*, shinier, silver spots not on intervals 2 or 4. Setae ed3 and ed5 located at anterior margin of silver spots; most specimens with at least one seta between elytral setae eo4 and eo5. Ventroapical setae of protarsomere 4 narrowly separated. Aedeagus of *B. argenteolum* generally larger, straighter, with a less evident ventrolateral bulge than *B. alaskense*. The only consistent difference noted was in the CSC flagellum: that of *B. argenteolum* has a narrower base and a less-sinuous dorsal margin. Duller than *B. semenovi*, with wider interval 3, and without lateral projection on male protarsomere 3.

Distinguished from the sympatric *B. velox* and *B. lapponicum* by the lack of midlateral pronotal setae, larger size, and (in some specimens) more distinct mirrors of elytral intervals 4 and 5.

This and the following two species form a taxonomically difficult complex of forms, which I call the *B. argenteolum*-subgroup. I follow Lindroth (1962, 1965) in treating it as three species (*B. argenteolum*, *B. alaskense*, and *B. semenovi*), although I am not entirely satisfied with this arrangement. *B. semenovi* is probably a distinct species, although it is possible that the holotype is simply an aberrant *B. argenteolum*. The distinctiveness of *B. alaskense* from *B. argenteolum* is more doubtful. While European *B. argenteolum* are quite different from Alaskan *B. alaskense*, the few specimens I have from the Lake Baikal region are somewhat intermediate (they are nearly the size of European *B. argenteolum*, but otherwise match Alaskan *B. alaskense*), suggesting that the distinct forms may simply be two extremes of one species. I discuss these specimens further under *B. alaskense*. However, the few specimens I have from the region between Lake Baikal and Alaska represent more typical *B. argenteolum*, indicating that the two forms are not simply ends of a cline. Because of this, and as the material before me from eastern Russia is rather meager, I will not synonymize the two names; more specimens from eastern Asia are needed to settle the problem.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.4–7.0 mm. Mirrors with dark brass, coppery-red, aeneous, or green reflection; rest of dorsal surface dark bronze, purple, or blue; mirrors of many specimens contrasted in color with rest of dorsal surface. Appendages mostly infuscated, piceous, with ventral portion of antennomere 1, venter at base of antennomeres 2 through 4, and base of femora rufous. Pronotum with shiny disc. Elytra shinier than that of *B. alaskense*, about as shiny as pronotum. Pronotum convex, with rounded margins. Elytra convex, humeral margins longer and more angulate than in many *B. alaskense*, nearly extended to stria 5; striae slightly to moderately impressed; interval 3 distinctly wider than 2. Spermatheca varied; cornu more or less curved in most specimens (Fig. 167). No posterior lobe at base of spermathecal duct. Stylomeres long, as in Figure 150.

Characteristics of First Instar Larva.

Description. See Andersen (1966) for more details about all larval stages. He includes information about only a few of the first instar characters I have studied. Head pale, centrally darker. Judging from his figures 12–14, setae PR_{13}, ME_{15}, and TE_{11} are long, and PR_{10} is apparently present and long.

Specimens Examined. I have seen 126 adults from the following collections: BMNH, CAS, DRMa, HNHM, MCZ, UMHF, USNM, ZMLS.

Geographic Distribution. Isolated on Ireland; on the mainland from western France and northern Italy, to Scandinavia, and eastward to the Lena River and Ussuri River regions of Russia (Fig. 263; Netolitzky and Meyer, 1933). The type specimen of *B. glabriusculum* is labelled "Sitka," presumably referring to Sitka, Alaska; this is probably an error, as no *B. argenteolum* are known from North America.

Geographic Variation. None noted over Europe and western Siberia. The one female I have examined from far eastern Russia ("Ussuri," UMHF), is more deeply microsculptured than other specimens, but otherwise appears to be a normal *B. argenteolum*.

Habitat. On barren or nearly barren sand banks of rivers or lakes (Lindroth, 1945).

Phylogenetic Relationships. Most closely related to *B. alaskense* or *B. semenovi*.

Bembidion alaskense Lindroth

Bembidion alaskense Lindroth, 1962:9. HOLOTYPE male examined, in CAS, labelled: "Grants Cabin, Toms Lake, Alask. Pen., Alask. VII-8-1919 [handwritten] / Van Dyke Collection / Holotypus alaskense Lth. [red label, partly in Lindroth's handwriting]." Type locality Lake Brooks (=Toms Lake [Orth, 1967]), Alaska Peninsula, Alaska.

Bembidion colvillense Lindroth, 1965:126. HOLOTYPE male examined, in MCZ, labeled: "Umiat, Alaska Aug. 6, 1958 George E. Ball / MCZ Holotype 32753 [red label] / Holotypus colvillense Lindroth [red label, in Lindroth's handwriting]." Type locality Umiat, Alaska. **New synonymy.**

Notes About Synonymy. The type of *B. colvillense* Lindroth is more heavily microsculptured than most southern *B. alaskense*, with the mirror on interval 4 thereby fainter. While this mirror is fainter than those on intervals 3 and 5, it is still distinct, contrary to Lindroth's (1965) statement; the striae are also not particularly regular. In the *B. colvillense* holotype the unpigmented nature of the aedeagus makes interpretation of its structure difficult, but in visible aspects it appears identical to *B. alaskense*. A sample from the Killick River (AMor, UASM!), not far from the type locality of *B. colvillense*, contains specimens similar to the *B. colvillense* type, the *B. alaskense* type, and a range of intermediates. It thus seems clear that all specimens from the Colville and Killick rivers belong to *B. alaskense*.

Derivation of Specific Epithet. From "Alaska," state of capture of the type series.

Characteristics of Adult. (Figs. 1, 8, 47, 50, 92, 110, 115, 132, 146, 151, 168.)

Diagnostic combination. Small (SBL = 5.0–6.3 mm, Alaskan specimens 5.0–5.7

mm); elytral mirrors on intervals 3 and 5, in some specimens on intervals 3 through 5, no distinct mirrors on intervals 6 and 7; pronotum lacking long basilateral carina, without midlateral seta; ventroapical setae of protarsomere 4 widely separated (Fig. 92); lateral projection on male protarsomere 3 lacking.

Comparisons with related species. Belongs to the *B. argenteolum*-subgroup. Distinguished from *B. argenteolum* by smaller size, and generally darker appendages. Prothorax in most specimens with disc shiny, otherwise the microsculpture is stronger than most *B. argenteolum*, and thus the surface is duller. Silver spots in many *B. alaskense* specimens larger, extended onto intervals 2 and 4. Seta of silver spot located nearer center of spot. Interval 9 of elytra generally lacking setae between eo4 and eo5. Ventroapical setae of protarsomere 4 widely separated. See also the "Comparisons with related species" section under *B. argenteolum*.

From *B. lapponicum* and *B. carinula* distinct in lacking the midlateral pronotal seta, and in having more definite mirrors on interval 5 (and generally also 4).

Description. See Table 2 for character states. Additional traits follow. SBL = 5.0–6.3 mm. Darker than *B. argenteolum*. Dorsal surface dark copper, bronze, aeneous, or bluish, mirrors in many specimens slightly purplish or reddish. Appendages dark, piceous or black, except for the venter of the antennomere 1, the base of femora, and the pro- and mesotrochanters, which are rufous; tibiae slightly paler in a few specimens, as is the maxillary palpomere 2. Pronotum narrower than *B. argenteolum*, sides straighter, not as rounded. Humeral margin short to medium-long, extended to stria 5 or not, generally not as angulate as in *B. argenteolum;* striae slightly to moderately impressed, in many specimens disrupted (especially 3 and 4); interval 3 wide, in many specimens abruptly widened just around silver spots. Spermatheca (Fig. 168) as for *B. argenteolum*, cornu of varied shapes. Stylomeres as in Figure 151.

Characteristics of First Instar Larva. (Figs. 212, 227, 233, 236.)

Diagnostic combination. Head capsule wide, diffusely darker centrally, frontale without traces of spots (Fig. 212); parietal denticles large, thin (Figs. 227, 233); PR_{13}, ME_2, ME_{14}, TE_6, TE_{11} long; abdominal segment VIII with EP_1 less than one-half width of EP_2.

Comparisons with related species. Distinguished from the other species with centrally dark head capsules, *B. carinula*, by the large setae ME_2 and TE_6, and the smaller, more widely distributed parietal denticles of *B. alaskense*.

Description. See Table 2 for character states. Additional traits follow. LHw = 490–500 μm, LHl = 340–365 μm, LCl/LHl = 0.110–0.118. Three specimens measured. Frontale without denticulate microsculpture (or at most with a few denticles around sensillum FR_b). Parietale lacking microsculpture near coronal suture. Mandible with prominent denticles dorsally near MN_1. Head wide, LHw/LHl = 1.35–1.47 (n = 3).

Characteristics of Second Instar Larva.

Description. LHw = 700–750 μm (n = 2). Frontale with extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens Examined. I have seen 157 adults, 156 first instars, 23 second instars, and 27 third instars from the following collections: AMNH, AMor, BMNH, CAS, CNC, DRMa, HNHM, MCZ, OSUC, OSUO, UASM, USNM, ZIL, ZMLS.

Geographic Distribution. Known from Alaska, from the Alaska Peninsula in the south to the Brooks Range in the north (Fig. 264); also in the region of Lake Baikal (Fig. 263).

Geographic Variation. While there is much within-population variation in Alaska, southern specimens seem in general to be darker, shinier, and with shorter appendages than specimens from north of the Brooks Range. Genitalic variation appears uncorrelated with external variation or geography. Specimens from Lake Baikal are larger than Alaskan specimens (SBL = 5.4–6.3 mm, mean = 5.86 mm, S.D. = 0.31, n = 7 for Njurga Bay, Lake Baikal; SBL = 5.0–5.7 mm, mean = 5.33 mm, S.D. = 0.26, n = 10 for Lake Brooks, Alaska), but otherwise possess all of the distinguishing features of *B. alaskense:* widely separated ventroapical setae of protarsomere 4, sinuate flagella, etc.

Habitat. On the bank of Lake Brooks, Alaska, larvae and adults were abundant on a barren, dark, volcanic-sand beach. On the north slope of the Brooks Range in northern Alaska, specimens were found under flood debris on the barren sand-silt bank of the Killick River (A. V. Morgan, pers. comm.), and on the mostly barren sand-clay bank of the Colville River (Lindroth, 1962:126).

Phylogenetic Relationships. A member of the *B. argenteolum*-subgroup, but beyond that its relationships are unclear (Figs. 292, 293).

Bembidion semenovi Lindroth

Bembidion semenovi Lindroth, 1965:127. HOLOTYPE male examined, in ZIL, labeled: "[handwritten label in Cyrillic, mostly indecipherable to me, ends in '8.VIII.910 A. Jacobson'] / Bracteon sp.n.? [handwritten] / B (Chrysobracteon) ?semenovi sp.nov. [handwritten] Kryzhanovskij det./ Holotypus semenovi Lth. [red label, partly in Lindroth's handwriting]." Type locality (Lindroth, 1965:127): Black Irtysh R., near the mouth of the Kaldzhir R. (=Markakol' R.), approximately 140 km NNE Zaisan, Siberia.

Derivation of Specific Epithet. Patronym given to honor the coleopterist André Semenov-Tian-Shanskij.

Characteristics of Adult. (Figs. 9, 78.)

Diagnostic combination. Large (SBL = 6.1 mm), convex, shiny; interval 3 narrow, with small silver spots (Fig. 9); appendages pale rufous or rufotestaceous; pronotum without long basilateral carina, without midlateral seta; male protarsomere 3 with lateral projection (Fig. 78).

Comparisons with related species. Belongs to the *B. argenteolum*-subgroup. Difficult to distinguish from some specimens of *B. argenteolum*. Shinier, with narrower interval 3, and smaller silver spots. Appendages paler than *B. argenteolum*, with antennomere 1 entirely rufotestaceous. Protarsomere 3 of male with lateral projection (Fig. 78). Male genitalia of the holotype is identical in all studied aspects to that of *B. argenteolum* specimens. See also the "Comparisons with related species" section under *B. argenteolum*.

Description. See Table 2 for character states. Additional traits follow. SBL = 6.1 mm. Dorsal surface aeneous, mirrors with coppery tint. Appendages very pale, entirely rufotestaceous, although antennomeres 3 to 11 and tarsi slightly infuscated. Disc of pronotum slightly shinier than in *B. argenteolum*. Elytra very shiny; mirrors on intervals 2 to 5, none on 6 or 7; mirrors only slightly shinier than the background; silver spots inconspicuous. Pronotum shaped as in members of *B. argenteolum*, that is, convex with rounded sides. Elytra convex, humeral margins moderately long, almost extended to stria 5; striae straight, moderately impressed; interval 3 narrow.

Characteristics of First Instar Larva. Unknown.

Specimen Examined. Only the holotype seen (ZIL).

Geographic Distribution. Known only from the type locality (Fig. 263).

Habitat. Unknown.

Phylogenetic Relationships. Most closely related to *B. alaskense* and *B. argenteolum* (Figs. 292, 293).

Bembidion stenoderum Bates

Bembidium stenoderum, Bates 1873:300. TYPE, not examined, BMNH. Type locality Osaka, Japan.

Bembidion uenoshiba Jedlička, 1965a:94. HOLOTYPE female, examined, in National Museum of Czechoslovakia, Prague. Labelled: "UENOSHIBA nr OSAKA VII-12 1947 COLL. Yosio Yano [partly handwritten] / TYPUS [bordered, reddish-gray] / Mus. Nat. Prague 23945 Inv. [orange label] / uenoshiba sp. n. [handwritten] det Ing. Jedlička [upper surface of label pink] / Bembidion stenoderum Bates det DR Maddison 1986." Type locality Uenoshiba (part of Osaka), Japan. **New synonymy**.

Bembidion stenoderum mukdensis Kirschenhofer, 1984:59. HOLOTYPE male, not examined, in Kirschenhofer collection, Vienna. Type locality Shenyang (Mukden), China.

Derivation of Specific Epithet. From the Greek *stenos,* meaning narrow, referring to the narrow body of members of this species.

Characteristics of Adult. (Figs. 10, 116, 133, 152, 169.)

Diagnostic combination. Small and narrow, body fusiform (Fig. 10); surface shiny, with mirrors on intervals 3 through 5, and in most specimens with faint mirrors on intervals 6 and 7; ed3 and ed5 in large pit; prothorax sides little rounded, with wide base, and midlateral seta absent; humeral margin long, extended to stria 5; striae deeply engraved; generally with two setae in ed7 area. Aedeagus slender, with straight basal portion and ventrally bent apex (Fig. 116); sclerite complexes far removed from basal orifice; right lobe of CSC ridged; ostial microtrichial patch very small.

Comparisons with related species. The fusiform shape and other characters mentioned in the diagnosis are distinctive; specimens are not likely to be misidentified.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.4–5.4 mm. Dorsal surface of body aeneous or bronze, mirrors purplish, silver spots bluish or aeneous. Appendages pale: most of antennomere 1 pale rufotestaceous, at least base of following three articles pale; legs infuscated at least at joints and on tarsi, slightly more generally infuscated in some examples. Sides of pronotum little sinuate, base wide (greatest width of prothorax at hind angles); basal tubercle relatively flat. Elytra tapered toward apex; humeral margins long, extended to inside stria 5; striae moderately to markedly impressed, more so than any other *Bracteon* (even stria 8 is more or less deepened throughout its length); stria 3 abruptly deeper around silver spots. Spermatheca varied, as in Figure 169; although cornu in some specimens shorter and straighter. Spermathecal duct without posterior lobe. Stylomeres as in Figure 152.

Characteristics of First Instar Larva. Unknown.

Specimens Examined. I have seen 44 adults from the following collections: BMNH, DRMa, HNHM, MCZ, UASM, USNM.

Geographic Distribution. Restricted to Japan and the neighboring mainland (Fig. 263).

Geographic Variation. None seen in the few specimens at hand from Japan. The only female I have seen from "China" (BMNH) is larger than average and quite dull. This form is considered a distinct subspecies (*B. s. mukdensis*) by Kirschenhofer (1984); I have not seen enough material to judge.

Habitat. Not known to me.

Phylogenetic Relationships. Unclear; may be related to *B. carinula* and relatives (Figs. 292, 293).

Bembidion carinula Chaudoir

Bembidium carinula Chaudoir, 1868:239. LECTOTYPE male designated by Lindroth 1963:237, in MNP, not examined. Type locality *"la Terre de Rupert,"* Rupert's Land, former name for the entire drainage basin of Hudson's Bay, thus including most of northern Québec, Ontario, Manitoba, etc. (Lamb, 1971); not Rupert House, Québec, as stated by Lindroth (1963).

Bembidion tuberculatum Notman, 1929:157. HOLOTYPE female, examined by Lindroth (1962), in Staten Island Museum. Type locality Marquette, Michigan, U.S.A.

Derivation of Specific Epithet. From the Latin *carina*, meaning "keel" or "ridge," presumably referring to the prominent basilateral carina of pronota of adults.

Characteristics of Adult. (Figs. 12, 70, 117, 134, 145, 154, 170, 185, 187, 188.)

Diagnostic combination. Pronotum with long, distinct basilateral carina extended to base (Figs. 12, 70), as well as a midlateral setae; elytral mirrors present on interval 3, in some specimens on intervals 4 and 5, but not on intervals 6 through 8; aedeagus slender, with narrow basal orifice (Fig. 117).

Comparisons with related species. From the externally similar *B. lapponicum* and

B. velox, males can be best separated by characters of the aedeagus, and females by the elongate second stylomeres (longer than 400 μm in *B. carinula*, around 200 μm in *B. velox* and *B. lapponicum*). Aedeagus of *B. carinula* slenderer, with narrower basal orifice; right lobe of CSC unridged; ostial microtrichial patch smaller; with no dorsal field; dorsal plate with small sclerotized patch with dark, irregular borders; other *Bracteon* have dark dorsal plates (most notably *B. hesperium*), but in these the sclerotized region is more extensive. *B. carinula* members can be externally distinguished from *B. lapponicum* by the long basilateral pronotal carina, more convex pronota with more-rounded sides and less-divergent hind angles, and relatively narrower elytral interval 3. From *B. velox*, by the pronotal carina.

Some specimens of *B. carinula* have been confused with *B. balli*, especially old, worn, *B. carinula* in which the mirrors are invisible or unclear; the basilateral pronotal carina and genitalia are the best distinguishing features.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.4–6.4 mm. Dorsal surface bronze, gray-bronze, coppery-red, dark bluish, or aeneous; mirrors in many specimens purplish or reddish; silver spots aeneous, blue, or bronze. Appendages in most specimens pale, with first four antennomeres rufotestaceous ventrally and basally, palpi partly pale, and legs rufotestaceous, femora and tibiae infuscated apically, tarsi dark. Other specimens, especially from Alberta and Saskatchewan, have the femur and tibia more extensively infuscated; in some only the bases of the femora are pale. In general, shinier than both *B. velox* and *B. lapponicum*. Pronotum frequently shinier than elytra. Mirrors on interval 5, when present, not more evident than on 4. Pronotum convex, sides sinuate, more definitely rounded than most specimens of *B. velox* or *B. lapponicum;* hind angle right or obtuse in many specimens. Humeral margins of elytra long, extended to stria 5 or nearly so; striae slightly to moderately impressed; interval 3 relatively narrow, not much wider than 2. Spermatheca as in Figure 170, with relatively short and straight cornu, and long, flat basal portion. Spermathecal duct with posterior lobe at base. Stylomeres as in Figure 154. Sternum X dark, asetose, clothed with small pegs (Fig. 185).

Characteristics of First Instar Larva. (Figs. 197, 198, 213, 228, 234, 243, 246, 250, 253, 256.)

Diagnostic combination. Head centrally darker, frontale without spots (Fig. 213); large, stout, closely set parietal egg bursters (Figs. 228, 234), PR_{13}, ME_{14}, and TE_{11} very short (Fig. 250); FR_1, FR_3, and segment VIII EP_1 as wide as nearby setae (Figs. 197).

Comparisons with related species. From the species with most similar larvae, *B. alaskense*, distinguished by the exceptionally large egg bursters and sensillar characters mentioned in the diagnosis.

Description. See Table 2 for character states. Additional traits follow. LHw = 450–460 μm, LHl = 340–360 μm, LCl/LHl = 0.094–0.104. Four specimens measured. Head pale with center diffusely darker, and with dark spot on center of frontale, or more generally pale brown. Frontale lacking pointed microsculpture (although two of the eight specimens studied had a few small denticles posteriorly). Mandibles lacking microsculpture (compare Fig. 198 with Figs. 199 and 239). Unlike most *Bracteon*, FR_5 is anterior to FR_4 in most specimens.

Characteristics of Second Instar Larva. (Fig. 260.)

Description. LHw = 630–665 μm (n = 2). Frontale with extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae short, less than two times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with ten long setae (Fig. 260).

Specimens Examined. I have seen 2,248 adults, 57 first instars, and 4 second instars from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, JKLi, KUSM, MCZ, OSUO, ROM, SAEl, SMNH, UASM, UBC, UCB, UMHF, UMSP, UMMZ, USNM, ZIL.

Geographic Distribution. A common species, distributed from Newfoundland and New Jersey in the east, south to Kentucky, west to Iowa, British Columbia, and north to southeastern Yukon and western N. W. T. (Fig. 265). I have seen three specimens, probably mislabeled, with the following labels: "Or." (USNM), "Tex" (MCZ), and "ARIZONA Pena Blanca 20.VIII.1966" (AMNH). Lindroth's (1963: 237) record from Washington is based on a misidentified *B. lapponicum* (OSUO!).

Geographic Variation. Populations from west of Manitoba have a higher frequency of dark appendages; those from northern British Columbia and southern Yukon in general are more heavily microsculptured, with less regular basilateral carinae of pronota, and less convex pronota.

Habitat. This species often occurs on upper, dry sand banks of rivers and lakes. In Manitoba and eastward, it seems restricted to lake banks, but occurs frequently along large rivers in Saskatchewan and westward.

Phylogenetic Relationships. Apparently related to *B. lapponicum* and *B. velox;* possibly the sister group of *B. stenoderum* (Figs. 292, 293).

Bembidion velox (Linné)

Carabus velox Linné, 1761:222. TYPE material lost (see Lindroth, 1957a:335, 339). Type locality Fårö Island near Gotland, Sweden.

Elaphrus impressus Panzer, 1797, number 8. Location of type unknown. Type locality Germany.

Elaphrus striatus Paykull, 1798:175 (not Fabricius, 1792:179). Type presumably in Paykull collection, Naturhist. Riksmus., Stockholm (Horn and Kahle, 1937). Type locality Sweden.

Bembidium Güntheri Seidlitz, 1891:64. Location of TYPE unknown, according to Lindroth (1962:13). Type locality Petrosavodsk, Russia.

(*Bembidion velox* v. *semicyaneum* Meier, 1899:97. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidium velox* L. ab. s. *bimaculatum* Uyttenboogaart, 1904:172 [not Kirby, 1837:52]. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidium velox* ab. *nigrescens* Kuhnt, 1913:57. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidion velox* ab. *moestum* Csiki, 1928:37; new name for *Bembidium velox* ab. *nigrescens* Kuhnt, 1913. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidion velox* ab. *Evertsi* Csiki, 1928:37; new name for *Bembidium velox* ab. s. *bimaculatum* Uyttenboogaart, 1904. [Name unavailable as clearly infrasubspecific.])

Derivation of Specific Epithet. From the Latin *velox*, meaning "swift," referring no doubt to the rapid running of members of this typical *Bracteon* species, and the speed with which they take flight.

Characteristics of Adult. (Figs. 13, 118, 135, 155, 171.)

Diagnostic combination. Elytral interval 3 with distinct mirrors, in some specimens on 2 through 5 as well; pronotum without long basilateral carina; if basilateral carina present, then short, not extended to pronotal base, midlateral seta present. Aedeagus with right lobe of CSC ridged and far removed from basal orifice (Fig. 118); ostial microtrichial patch extended dorsally as a prominent dorsal field of long microtrichia; left-most central membranes with small, sparse, heavily sclerotized scales, sac thus with a peppered appearance; "pillow" with large scales lacking.

Comparisons with related species. The short basilateral carina of pronotum, isolated from the base, distinguishes adults of this species from those of *B. carinula*. As well, the elytra of *B. velox* are generally narrower and more nearly parallel-sided. Aedeagal characters of *B. velox*, as noted in the diagnoses, are also distinctive. Differences from *B. lapponicum* are given under that species.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.6–6.0 mm. Dorsal surface dull bronze, coppery, aeneous, or bluish; mirrors coppery red or purplish, silver spots aeneous, bluish, or bronze. Appendages in most specimens pale; antennomere 1 entirely pale, or infuscated dorsally, antennomeres 2 through 4 pale basally; palpi dark apically, maxillary palpomere 2 pale; legs rufous, slightly infuscated at joints and on tarsi. Pronotum similar to that of *B. carinula*, with sides less rounded in most specimens. Humeral margin of elytra long, to interval 5 or beyond; striae slightly to moderately impressed; interval 3 relatively narrow. Spermatheca with short, apically hooked cornu, more tapered than in *B. lapponicum;* basal portion long, flat (Fig. 171). Spermathecal duct with no posterior lobe. Stylomeres as in Figure 155.

Characteristics of First Instar Larva. Unknown.

Specimens Examined. I have seen 195 adults from the following collections: AMNH, BMNH, CAS, CNC, HNHM, ICCM, MCZ, UMHF, USNM, ZMLS.

Geographic Distribution. In the Palearctic from western France to Scandinavia, north of the Alps, east to the Irtysh and Jenesei Rivers of Russia, and Shenyang, China (Netolitzky and Meyer, 1939; Lindroth, 1962; Fig. 266; Kirschenhofer, 1984).

Geographic Variation. None observed.

Habitat. On pure, completely barren sand (Lindroth, 1945). On larger lakes and river banks; also on banks of bodies of salt water (for example, the Baltic Sea [Lindroth, 1945]).

Phylogenetic Relationships. The inconclusive evidence available suggests a relationship with *B. carinula*, and possibly *B. stenoderum* (Figs. 292, 293).

Bembidion *lapponicum* Zetterstedt

Bembidium impressum Var. B. *lapponicum* Zetterstedt, 1828:6. LECTOTYPE male selected by Lindroth, 1963:239, in UML. Type locality Vittangi on Torne-älve, Sweden.

Bembidium latiusculum Motschulsky, 1845:272. TYPE material apparently lost, according to Lindroth (1962:13); Keleinikova (1976) does not include this name in her catalogue of the Motschulsky collection in Moscow. Type locality "en Dauria et au Kamtchatka," restricted to "'Dauria', that is Transbaicalia, Siberia" by Lindroth (1962:13).

Bembidium Jenisseense J. Sahlberg, 1880:14. LECTOTYPE female selected by Lindroth, 1963:239, in UMT. Type locality Imbatsk, Lower Jenissei, Russia.

Bembidium pugetanum Fall, 1916:13. HOLOTYPE male, examined, in MCZ. Labeled: "Seattle Wash O.B.J. [handwritten] / TYPE pugetanum / M.C.Z. Type 23865 [red label] / H. C. FALL COLLECTION." Type locality Seattle, Washington.

Derivation of Specific Epithet. From "Lapponia," or Lapland.

Characteristics of Adult. (Figs. 14, 44, 46, 51, 59, 61, 71, 119, 136, 156, 172.)

Diagnostic combination. Elytra with mirrors on interval 3, in most specimens with fainter mirrors on 2 through 5, rarely with very faint mirrors on 6 and 7; pronotum without long basilateral carina, with midlateral seta, and with hind angles prominent, flared outward (Fig. 14); aedeagus wide and short, with one prominent apical lobe (the "pillow") with large triangular scales (Fig. 119).

Comparisons with related species. Difficult to distinguish using external characters from *B. velox*, and to a lesser extent, *B. carinula*. The prothorax of *B. lapponicum* is flatter, with less rounded sides, and broader base with more protruded hind angles. Generally silver spots are wider and longer, with interval 3 wider as well. Legs are darker in most specimens. Aedeagus wider and much shorter than in *B. velox* and *B. carinula;* right lobe of CSC ridged as in *B. velox*, but the lobe is more basal, nearly touching the basal orifice; ostial microtrichial patch large, posteriorly with many comb-like scales extended upward as the dorsal field; central membranes not peppered, as scales are larger and less sclerotized; apically, the "pillow" is covered with large triangular scales; other *Bracteon* have similarly positioned lobes, but no other has such distinctive scales.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.5–6.1 mm. Dorsal surface bronze, gray-bronze, bluish, or aeneous; mirrors purplish or coppery; silver spots aeneous, bluish, or bronze. Appendages dark, piceous, except for venter of antennomere 1, and femur at base, which are rufous or rufopiceous; some specimens have as well paler tibiae. Midlateral setae of pronotum present, rarely absent; only one specimen seen (from "Maalselven, Framnes," ZMLS!) without setae. Side margins of pronotum sinuate, little rounded, hind angles prominent, flared outward, acute in most specimens; basilateral carina thin, generally short, never extended to basal edge of pronotum. Humeral margin of elytra long, extended to inward of stria 5, longer than in *B. carinula;* striae slightly to moderately impressed; interval 3 wide, especially around silver spot. Spermatheca with long, distinctly curved cornu; basal portion long, flat (Fig. 172). Spermathecal duct with or without small posterior lobe. Stylomeres as in Figure 156.

Characteristics of First Instar Larva. (Figs. 206–209, 214, 229, 235.)

Diagnostic combination. Head capsule dark, without traces of spots on frontale (Fig. 214); prominent parietal denticles (Figs. 229, 235); setae ME_2 and TE_6 short, scale-like; seta ST_2 on segment IX present.

Comparisons with related species. From the similarly dark *B. balli* and *B. foveum*, distinguished by the shorter coronal suture and more prominent parietal denticles, as well as the short ME_2 and TE_6.

Description. LHw = 400–425 μm, LHl = 330–350 μm, LCl/LHl = 0.114–0.129. Three specimens measured. Head capsule dark, piceous, more or less uniform, or frontale darker centrally, paler laterally; parietale darker in front of PA_4 and PA_7.

Characteristics of Second Instar Larva. (Fig. 259.)

Description. LHw = 540 μm (n = 1). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae short, less than two times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with nine long setae (Fig. 259).

Specimens Examined. I have seen 366 adults, 33 first instars, and 2 second instars from the following collections: AMNH, AMor, BMNH, CAS, CNC, DRMa, HNHM, ICCM, MCZ, OSUC, OSUO, UASM, UMHF, USNM, ZMLS.

Geographic Distribution. A widespread Holarctic species (Fig. 267; Lindroth, 1962), in the Old World from northernmost Scandinavia throughout much of Russia, south to Mongolian Peoples' Republic, east to Kamtchatka. In North America (Fig. 267b) common in the northwest, from Alaska east to the Anderson River; uncommon at scattered localities in the south from Washington, Oregon, Idaho, and Wyoming, east to central Saskatchewan.

Geographic Variation. Populations from the southern portion of the range in North America (central B. C., Alberta, and Saskatchewan southward) are more uniform than northern populations. Southern specimens are larger, with straighter, less-impressed striae, a generally smoother and shinier surface, with mirrors on intervals 2, 4, and 5 generally absent or very faint, and with a relatively narrow interval 3; some northern specimens are like this as well. The male genitalia appear identical to those of northern specimens. Unfortunately, the relative lack of collecting throughout much of the northern portions of British Columbia, Alberta, and Saskatchewan makes interpretation of this form difficult: it is unknown if the southern form is allopatric or sympatric with the northern form, or if a cline connects them. Further work may reveal the distinctiveness of the southern form, if so, it would take on the epithet "*pugetanum* Fall," most likely as a subspecies of *B. lapponicum.* The material I have at hand is too limited to identify clear patterns of variation in the Old World. Lindroth (1962) gives a brief discussion of Palearctic variation.

Habitat. Generally on barren sand banks of large rivers, less frequently around small rivers, and rarely around lakes (Lake Brooks, Alaska).

Phylogenetic Relationships. Perhaps part of a clade with *B. velox*, *B. stenoderum*, and *B. carinula* (Figs. 292, 293).

Bembidion punctatostriatum Say

Bembidium punctato-striatum Say, 1823b:83. NEOTYPE male designated by Lindroth and Freitag (1969:335), examined, in MCZ, labeled: "Rumney, N.H. V.51 Lindroth / Neotypus Bembidium punctatostriatum Say design Lth [red label, in Lindroth's handwriting] / Bembidion punctatostriatum Say det. Lindroth 68." Type locality Rumney, New Hampshire, designated by Lindroth, 1962:12.

Bembidium sigillare Say, 1834:437. TYPE material lost, see Lindroth and Freitag (1969:335). Type locality "Missouri" (probably present-day Nebraska, according to Lindroth, 1969:1113).

Bembidium stigmaticum Dejean, 1831:83. TYPE, examined by Lindroth (1962:12), in MNP. Type locality: "Amérique septentrionale."

Derivation of Specific Epithet. From the Latin *punctum*, meaning puncture, and *stria*, meaning furrow or line, referring to the punctate striae of this species.

Characteristics of Adult. (Figs. 11, 33, 34, 45, 48, 52, 60, 67, 72, 94, 120, 137, 153, 173.)

Diagnostic combination. Long and wide (Fig. 11); surface shiny, mirrors present on interval 3, but not on 6 and 7; mentum tooth parallel-sided, truncate, bulbous; prothorax with wide base and little-rounded sides (Fig. 11), with midlateral seta; humeral margin of elytra prominent, long, extended to stria 5 (Fig. 72); ostial patch of simple microtrichia large (Fig. 120).

Comparisons with related species. A distinctive species, not liable to be confused with other species. From the somewhat similar *B. lorquinii* distinguished externally by the wider body and presence of midlateral pronotal seta, and aedeagally by the usually unridged right CSC lobe and the prominent dorsal VSP ridge.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.9–7.1 mm, rarely below 5.5 mm. Dorsal surface bronze or silver gray, mirrors coppery red or purplish, silver spots aeneous. Antennomere 1 ventrally pale; legs dark, piceous or black, with base of femora, pro- and mesotrochanters, as well as tibiae in most specimens, rufous or rufopiceous. Pronotum with slightly sinuate sides and wide base (about as wide as maximum width anterior to hind angles). Elytral humerus prominent, with long margin, extended to stria 5; striae shallow to moderately impressed. Spermatheca quite varied, in many specimens as in Figure 173; cornu curved or not, generally fairly long. Spermathecal duct with distinct bulb at base, but no posterior lobe. Stylomeres as in Figure 153.

Characteristics of First Instar Larva. (Figs. 194, 204, 215, 230, 237, 239, 241, 251, 254.)

Diagnostic combination. Head broad, pale, with 3-spotted frontale and 2-spotted parietale (Fig. 215); parietal denticles small; seta FR_3 thick but FR_1 thin; pronotum with extensive tubercles set in rows; basilateral corners of thoracic tergites with several extra small setae (setal groups gPR and gME, Figs. 237, 241), and posterolateral corner of abdomen with extra seta (TE_α, Fig. 251).

Comparisons with related species. The distinctly spotted head, microtuberculate pronotum, and setal groups gPR and gME combine to make *B. punctatostriatum* first instar larvae distinctive and unlikely to be misidentified.

Description. See Table 2 for character states. Additional traits follow. LHw = 440–505 μm, LHl = 370–390 μm, LCl/LHl = 0.128–0.130. Three to five specimens measured.

Characteristics of Second Instar Larva.

Description. LHw = 730 μm (n = 1). Frontale without extra setae near FR_3, and with microsculpture posteriorly. Head and pronotum with accessory microsetae less than two times longer than wide. Microsculpture present centrally on pronotum. Urogomphus with seven long setae.

Specimens Examined. I have seen 425 adults, 70 first instars, 1 second instar, and 1 third instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, ICCM, JKLi, KUSM, MCZ, OSUC, OSUO, ROM, SMNH, UASM, UBC, UMMZ, USNM, ZIL.

Geographic Distribution. In the New World from New Brunswick and Maine south to Kentucky and Arkansas (Lindroth, 1962); in the west from Saskatchewan and Montana, to the Yukon, and Fort MacPherson, N. W. T.; apparently absent from the center of the continent (Fig. 268). I have seen three specimens labelled "TEX" (OSUC, USNM), and two labelled "Cal." (MCZ); both are doubtful records.

Geographic Variation. None noted.

Habitat. On the barren sand banks of large and small rivers, as well as lakes. Specimens frequent drier areas of the sand banks; on the North Saskatchewan River near Paynton, Saskatchewan, found at a considerable distance from the water.

Phylogenetic Relationships. B. punctatostriatum has proven to be the most difficult *Bracteon* to place phylogenetically. It shows characters linking it with the *B. argenteolum*-subgroup, *B. lapponicum*, and the *B. inaequale*-subgroup. It is more likely related to *B. lapponicum* and its relatives (Figs. 292, 293).

Bembidion hesperium Casey

Bembidium hesperum Fall, 1910:95 (not Crotch, 1867: 385). HOLOTYPE male, examined, in MCZ. Labeled: "Vanc. Id. 8/24/96 / hesperum TYPE [handwritten] / M.C.Z. Type 23862 [red label] / H.C. Fall Collection." Type locality Vancouver Island, British Columbia.

Bembidion hesperium Casey, 1918:9. New name for *B. hesperum* Fall.

Bembidion binarium Casey, 1918:9. LECTOTYPE male designated by Lindroth, 1975:115, in USNM. Type locality: California.

Derivation of Specific Epithet. From the Latin *hesperius*, meaning "western" or "of the evening." This lovely name might refer to either the place of residence of these animals, the western edge of North America, or to their dark tone.

Characteristics of Adult. (Figs. 15, 53, 64, 95, 121, 138, 157, 174.)

Diagnostic combination. Dark, shiny; mirrors thus somewhat obscured (Fig. 15), present on intervals 3 through 5; dorsal surface of elytra with sculpticells generally transverse (isodiametric only in deeply microsculptured females) (Fig. 64); pronotum with carina short or absent, lacking midlateral seta; stria 3 abruptly deeper around silver spots; basal portions of femora rufous; aedeagus with wide apex, right CSC lobe at most slightly ridged (Fig. 121).

Comparisons with related species. Adults of this species are the darkest *Bracteon*, and, along with *B. semenovi*, the shiniest. Most similar to *B. lorquinii*, with which it shares the lack of the midlateral seta of the pronotum. Besides luster, color, and genitalia, specimens can be distinguished by the more deeply engraved and punctate striae, smaller size, and proportionally wider body. Genitalic differences are described under *B. lorquinii* .

Description. See Table 2 for character states. Additional traits follow. SBL = 4.7–5.8 mm. Dorsal surface dark, with aeneous, bluish green, or bronze tint; mirrors coppery or purplish red; silver spots aeneous or bluish green. Appendages dark, for the most part piceous; antennomere 1 rufous ventrally; in most specimens basal portions of femora are rufous as well. Pronotum with sides slightly sinuate. Elytral humerus somewhat rounded, margin short, extended to stria 6 but not 5; striae slightly to moderately impressed; third deepened abruptly around silver spots. Spermatheca as in Figure 174; cornu fairly short, only slightly curved. Spermathecal duct without posterior lobe. Stylomeres as in Figure 157.

Characteristics of First Instar Larva.

Diagnostic combination. As for *B. lorquinii*, except that there is virtually no microsculpture near coronal suture. No other differences noted. LHw = 350–360 μm, LHl = 255–270 μm, LCl/LHl = 0.109–0.111. Two specimens measured. See Table 2 for full description.

Characteristics of Second Instar Larva.

Description. As for *B. lorquinii;* LHw = 540 μm (n = 2).

Specimens Examined. I have seen 417 adults, 52 first instars, 7 second instars, and 1 third instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, MCZ, OSUO, UASM, UBC, USNM, ZIL.

Geographic Distribution. Restricted to the westernmost states, from around San Francisco, California, north to Washington, and in southernmost British Columbia (Fig. 269).

Geographic Variation. Specimens from the south (e.g., Klamath River, northern California, DRMa!) tend to be shinier, with more-transverse elytral sculpticells, and with flatter pronota with less rounded sides than specimens from the north (e.g., Nooksack River, northern Washington, DRMa!).

Habitat. Known only from the sandy banks of rivers; occasionally among vegetation.

Phylogenetic Relationships. A relatively basal member of the 2n = 20+XY clade; its sister group is not known (Figs. 292, 293).

Bembidion lorquinii Chaudoir

Bembidium lorquinii Chaudoir, 1868:239. LECTOTYPE male designated by Lindroth, 1963:235, in MNP. Type locality California.

B. lorquini auctorum.

Bembidion tacomae Casey, 1924:22. LECTOTYPE male designated by Lindroth, 1975:115, examined, in USNM. Labeled: "Wawawai Wn [handwritten] / CASEY bequest 1925 / TYPE USNM 36797 [red label] / tacomae Csy [handwritten] / LECTOTYPE tacomae Csy By C. H. Lindroth." Type locality Wawawai, Washington.

Notes About Synonymy. "*Bembidion lorquini*" is an incorrect subsequent spelling (ICZN, Third edition, Article 33[d]).

Derivation of Specific Epithet. Patronym honoring M. Lorquin, who sent the type series to M. H. Deyrolle, from whom Baron Chaudoir received them.

Characteristics of Adult. (Figs. 16, 122, 139, 158, 175.)

Diagnostic combination. Duller than *B. hesperium* (Fig. 16), with mirrors on intervals 3 through 5; elytral sculpticells isodiametric; pronotum with carina short or lacking, and without midlateral seta; stria 3 not as abruptly deepened around silver spots; femora black or piceous; aedeagus with ridged right CSC lobe, otherwise as in Figure 122.

Comparisons with related species. A large species, similar to *B. hesperium*. It is larger, more slender, and with a duller luster than specimens of that species. In addition, the striae of *B. lorquinii* are shallower, especially around the silver spots, and the punctures are smaller; ed3 and ed5 in smaller pit than in *B. hesperium;* apex of aedeagus narrower than in *B. hesperium;* right lobe elongate, consistently markedly ridged (at most only slightly so in *B. hesperium*); ostial microtrichial patch larger than in *B. hesperium,* with more extensive dorsal field; VSP with slightly more prominent, angulate dorsal ridge.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.3–6.8 mm. Dorsal surface greenish-gray, gray-bronze, or bronze; mirrors purplish, coppery, or bronze; silver spots grayish, bronze, or aeneous. Appendages very dark, black or piceous, with only the pro- and mesotrochanters paler, rufopiceous. Pronotal side margins little sinuate; basilateral tubercle prominent. Humeral margins of elytra short, extended to stria 6 but not 5; striae slightly to moderately impressed, not abruptly deepened around silver spots. Spermatheca varied, in many specimens as in Figure 175. Spermathecal duct without posterior lobe. Stylomeres as in Figure 158.

Characteristics of First Instar Larva. (Fig. 216.)

I have not been able to distinguish larvae of *B. lorquinii* from most members of the *B. inaequale*-subgroup. The description below thus applies, with a few exceptions, to *B. lorquinii*, *B. zephyrum*, *B. levettei*, and *B. inaequale*.

Diagnostic combination. Head pale, with 3-spotted frontale, spots indistinct in some specimens (Fig. 216); parietale with small denticles, with denticulate microsculpture near coronal suture; pronotum lacking microsculpture; ME_2 and TE_6 large.

Comparisons with related species. *B. lorquinii* and *B. inaequale*-subgroup larvae are most similar to those of *B. balli* and *B. foveum*. However, the former have paler head capsules, with more prominently denticulate frontales, and lack lateral pronotal microtubercles.

Description. See Table 2 for character states. Additional traits follow. LHw = 380–390 μm, LHl = 295–300 μm, LCl/LHl = 0.119–0.133. Two specimens measured.

Characteristics of Second Instar Larva.

Description. LHw = 550 μm (n = 1). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens Examined. I have seen 389 adults, 16 first instars, and 2 second instars from the following collections: AMNH, BHar, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, HNHM, ICCM, JKLi, MCZ, OSUO, UASM, UBC, UCB, UMMZ, USNM, ZIL.

Geographic Distribution. Similar to that of *B. hesperium*, but with an extension farther eastward. From near Los Angeles, California, east to western Nevada, north to Idaho and southwesternmost British Columbia (Fig. 270). I view the record from Colorado (Lindroth, 1963, USNM!) with suspicion.

Geographic Variation. None noted.

Habitat. Generally found on barren sandy banks of rivers. One population has been found near seepage on sandy Wreck Beach, on the Pacific Ocean banks of Vancouver, B. C. (BHar!). The water here is at least brackish, if not saline (B. Harrison, pers. comm.), making this population the only known *Bracteon*, other than *B. zephyrum* and *B. velox*, found next to salty water.

Phylogenetic Relationships. B. lorquinii belongs to the 2n = 20+XY clade, but its precise relationships with *B. hesperium* and the *B. inaequale*-subgroup are unresolved (Figs. 292, 293).

Bembidion zephyrum Fall

Bembidium zephyrum Fall, 1910:96. HOLOTYPE male, examined, in MCZ. Labeled: "Humboldt Co. CAL. / [male symbol] / zephyrum TYPE [handwritten] / M.C.Z. Type 23870 [red label] / H.C. Fall Collection / Bembidium zephyrum Fall." Type locality Humboldt County, California.

Bembidion zephyrum tristiculum Casey, 1924:22. LECTOTYPE male designated by Lindroth, 1975: 115, examined, in USNM. Labeled: "S. Oregon Kunf [spelling?] [handwritten] / CASEY bequest 1925 / TYPE USNM 36795 [red label] / tristiculum Csy [handwritten] / LECTOTYPE sbsp. tristiculum Csy By C. H. Lindroth." Type locality southern Oregon.

Bembidion marginosum Casey, 1924:23. LECTOTYPE male designated by Lindroth, 1975:115, examined, in USNM. Labeled: "Del Norte Co. CAL VI.2.10 / CASEY bequest 1925 / marginosum Csy [handwritten] / TYPE USNM 36793 [red label] / LECTOTYPE marginosum Csy By C. H. Lindroth." Type locality Del Norte County, California.

Derivation of Specific Epithet. From the Latin *zephyrus*, meaning "west wind." The beaches these beetles inhabit are swept over by winds blowing from the west across the Pacific Ocean.

Characteristics of Adult. (Figs. 19, 54, 79, 82, 84, 123, 140, 159, 176.)

Diagnostic combination. Wide, relatively flat; with prominent raised mirrors on intervals 2 through 7, in pattern of Figure 19; connection between anterior elytral mirrors and central mirrors absent or consisting of only a very thin mirror on interval 3; pronotum with carina small or absent, with wide lateral expansion and flared front angles; midlateral pronotal seta present; aedeagus with very broad ostial microtrichial patch; VSP with rounded, unscaled dorsal ridge (Fig. 123).

Comparisons with related species. Rather similar to *B. levettei*, with which it has been confused in the past. Specimens of *B. zephyrum* are generally brighter than those of *B. levettei*, with the copper or purple mirrors contrasted against the generally green or blue-green elytra. The mirror of the anterior portion of intervals 3 through 5 is connected to the more posterior mirrors only by a faint band on the interval 3 (Fig. 19); in related species (for example, *B. levettei*, Fig. 20) this band is a much more definite mirror. Mentum tooth not bulbous, against *B. levettei* and *B. inaequale;* incisions in mentum not as deep or outwardly directed as in *B. levettei* and *B. inaequale;* submentum with 4 setae, with medial setae absent, in contrast to 6 setae in *B. levettei*. The side margin of the pronotum is more explanate than in most specimens of related species; it flares out into a protruded front angle. Protarsomere 1 of males is noticeably wider and thicker than in *B. levettei* (compare Figs. 79 and 82 with 80 and 83), as are the associated adhesive setae (compare Fig. 84 with 85). Ostial microtrichial patch extensive, with apical comb-like scales, and a prominent dorsal field of microtrichia. VSP usually without the distinctly angulate and sclerotized dorsal ridge of *B. levettei* and other members of the group, dorsal ridge not angulate.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.0–6.3 mm. Dorsal surface generally bluish green, although some specimens aeneous, with purplish, coppery red, or purplish black mirrors; this same contrast in color between shiny and dull areas of the elytra is also true of the pronotum. Appendages dark, piceous except for rufous pro- and mesotrochanters and base of femora. Pronotum with distinct shiny band on disc on each side close to midline; in some females outer mirrors rather faint, or, rarely, virtually absent (one female from Siltcoos Outlet, Oregon, OSUC!); interval 7 mirror connected to inner mirrors, although the connecting interval 6 mirror is occasionally faint or small. Pronotum wide, relatively flat, lateral margins expanded as protruded front angles. Elytral humerus somewhat rounded, short, not extended to stria 5; striae slightly to moderately impressed. Spermatheca as in Figure 176; cornu distinctly curved. Spermathecal duct without posterior lobe. Stylomeres as in Figure 159, of varied lengths (Fig. 3).

Characteristics of First Instar Larva. (Fig. 217.)

Diagnostic combination. As for *B. lorquinii*, except color paler, flavous; head generally, but not always, with distinct spotted pattern. LHw = 380–410 μm, LHl = 315–320 μm, LCl/LHl = 0.117–0.119. Two specimens measured. See Table 2 for full description.

Characteristics of Second Instar Larva.

Description. As for *B. lorquinii*.

Specimens Examined. I have seen 1,162 adults, 22 first instars, and 1 second instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, HNHM, MCZ, OSUO, UASM, UBC, UCB, UMSP, UMMZ, USNM, ZIL.

Geographic Distribution. Found mainly on the Pacific coast of North America, from San Francisco to the Queen Charlotte Islands (Fig. 271); only a few specimens have been found at inland localities. Inland specimens from Creston, B. C., reported by Lindroth (1962, 1963) as *B. zephyrum*, are actually members of *B. levettei levettei* (CNC, UBC!).

Geographic Variation. None noted in external features. However, the length of S2 in females varies considerably (from 190 μm to 325 μm); this variation is correlated with geography (Fig. 3), but apparently not with body size (although careful measurements to support this claim are lacking). Except for the only two known *B. zephyrum* females from central California (San Francisco) (CAS!), Californian specimens have shorter S2s than do specimens from Bandon, Oregon, and northward; southernmost Oregon is a zone of intermediates.

Habitat. For the most part restricted to sandy beaches of the Pacific Ocean, where it is sometimes abundant under driftwood.

Phylogenetic Relationships. A relatively basal member of the extensively mirrored *Bracteon* (Figs. 292, 293).

Bembidion levettei Casey

Bembidion levettei Casey, 1918:9. LECTOTYPE male designated by Lindroth, 1975:114, examined, in USNM. Labeled: "Col / CASEY bequest 1925 / TYPE USNM 36793 [red label] / levettei Csy [handwritten] / LECTOTYPE levettei Csy By C. H. Lindroth." Type locality Colorado.

Bembidion carrianum Casey, 1924:23. LECTOTYPE female designated by Lindroth, 1975:115, examined, in USNM. Labeled: "Edmonton Alta 1.VII.1920 F.S. Carr / CASEY bequest 1925 / carrianum Csy [handwritten] / TYPE USNM 36800 [red label] / LECTOTYPE carrianum Csy By C. H. Lindroth." Type locality Edmonton, Alberta.

Derivation of Specific Epithet. Patronym honoring G. M. Levette, a physician and amateur entomologist who collected the type specimen (Ewan, 1950). *Bembidion carrianum* Casey, treated here as a subspecies of *B. levettei*, is a patronym honoring the amateur coleopterist F. S. Carr.

Characteristics of Adult. (Figs. 20, 21, 55, 80, 83, 85, 103–106, 111, 124, 125, 141, 160, 161, 177, 180–182.)

Diagnostic combination. Mirrors on intervals 2 through 7, in pattern of Figures 20, 21; anterior elytral mirrors generally connected to middle mirrors by a broad mirror on interval 3; mirrors on intervals 6 and 7 located nearer anterior silver spot, broadly connected to inner mirrors; pronotum with carina short or absent, front angle not flared outward, midlateral seta present; VSP with both basins and dorsal ridge scaled (a few specimens lack or have only very small scales) (Figs. 124, 125).

Comparisons with related species. This and the following three species form the *B. inaequale*-subgroup. They share extensive elytral mirrors, straight CSC flagella, 10 pairs of autosomal chromosomes, and similar larvae.

Many specimens confused with the other two North American species with mirrors on elytral intervals 6 and 7, *B. zephyrum* and *B. inaequale*. Distinguished from *B. zephyrum* by characters mentioned under that species's account. As well, leftmost central membranes of internal sac with large, heavily sclerotized scales, unlike those found in *B. zephyrum*. From *B. inaequale* distinct in having the outer mirrors near the anterior silver spot; these outer mirrors are generally connected to the inner mirrors in *B. levettei*.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.8–6.1 mm. Dorsal surface greenish-gray, aeneous, or bronze; mirrors purplish, reddish, or coppery; silver spots greenish-gray, aeneous, or bronze. Appendages dark, piceous except extreme base of legs and (in a few specimens only) venter of antennomere 1 rufous. Pronotum with distinctly contrasted shiny discal band near midline present or faint; with a small "silver spot" near the lateral edge of this band. Sides of pronotum moderately sinuate. Humeral margins of elytra short, not extended to stria 5; striae slightly to moderately impressed. Spermatheca varied; with very long cornu, slightly to distinctly curved, basal portion short (Fig. 177). Spermathecal duct without posterior lobe. Stylomeres as in Figures 160, 161; no consistent differences observed between the subspecies.

Characteristics of First Instar Larva. (Fig. 231.)

Diagnostic combination. As for *B. lorquinii*. LHw = 380–420 μm, LHl = 315–355 μm, LCl/LHl = 0.137–0.155. Six specimens measured. See Table 2 for complete description.

Characteristics of Second Instar Larva. (Fig. 218.)

Description. As for *B. lorquinii*. LHw = 580–625 μm (n = 2).

Specimens Examined. I have seen 1,606 adults, 36 first instars, 9 second instars, and 1 third instar from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, ISAs, JKLi, KUSM, MCZ, OSUO, ROM, SMNH, UASM, UBC, UMSP, UMMZ, USNM, ZIL.

Geographic Distribution. B. levettei levettei is found in the western mountains, from southern British Columbia and southwestern Alberta to Idaho, Wyoming, Colorado, and northernmost New Mexico (Fig. 272). I have seen as well one specimen from Washington, and another labelled "Cal." (MCZ!). *B. levettei carrianum* is transamerican, from Newfoundland and Labrador west through Minnesota to central Alberta, British Columbia, and north into Alaska and N. W. T. (Fig. 272).

Geographic Variation. This variable species consists of two distinct forms, which I treat as subspecies, *B. levettei levettei* and *B. levettei carrianum.* The two forms are, as far as known, allopatric, with no signs of intergradation (although intermediate localities have not been well collected). One form is strictly southern and montane, and the other almost exclusively more northern or lowland (Fig. 272). The only exceptions I have seen are three specimens from Fort Collins, Colorado (CAS!). Two of these males have genitalia of the *B. levettei carrianum* form, and yet they are within the known range of *B. levettei levettei*, far from the range of *B. levettei carrianum.* The third male is genitally intermediate between the two subspecies. The significance of these three specimens is uncertain; more material is needed from northern Colorado.

Bembidion levettei levettei specimens are distinguished from *B. levettei carrianum* primarily by male genitalia: members of *B. levettei levettei* lack the basodorsal lobe of the internal sac possessed by members of *B. levettei carrianum* (compare Fig. 125 with 124) (46 specimens of *B. levettei levettei* examined, 66 of *B. levettei carrianum*). In inverted internal sacs, this lobe of *B. levettei carrianum* is manifest as a characteristic bulge of the anterior edge of the ostial cavity (Fig. 103, arrow). *B. levettei levettei* aedeagi are generally larger, more curved ventrally, with a wider apex, but there are exceptions to these characters. However, there are a few somewhat consistent differences in external characters. Members of *B. levettei levettei* tend to be larger and shinier than *B. levettei carrianum*, with the mirrors more contrasted in luster and color to the surrounding surface. This includes not only the mirrors of the elytra, but also the shiny areas of the pronotum, which are generally a shiny purplish contrasted against the dull grayish green of the rest of the pronotum. Mirrors on elytral intervals 5 through 7 tend to be a bit more extensive, and are positioned slightly more posteriad (compare Fig. 20 with 21). The striae of *B. levettei levettei* are a bit deeper (at least in northern populations). The elytra are slightly more parallel-sided, and relatively larger than the pronotum; the sides of the pronotum are less rounded (Fig. 20). Stria 4 is more frequently straight in *B. levettei levettei.* Most of these external characters are rather vague, and none consistently distinguish the two subspecies.

Habitat. B. levettei members are found most commonly on barren sand or sand-silt banks of rivers; also on creek and lake banks.

Phylogenetic Relationships. The relationships within the *B. inaequale*-subgroup are unclear (Figs. 292, 293); indeed, I am not certain that the two subspecies of *B. levettei* are themselves sister taxa.

Bembidion inaequale Say

Bembidium inaequalis Say, 1823a:151. NEOTYPE male designated by Lindroth and Freitag (1969: 335), examined, in MCZ, labeled: "Mt Pleasant Ia Apr 28 1934 Knutson / inaequale det. Darlington / Neotypus Bembidium inaequale Say design Lth [red label, in Lindroth's handwriting] / Bembidion inaequale Say s.str.det. Lindroth 68." Type locality Mount Pleasant, Iowa.

Bembidium arenarium Dejean, 1831:80. TYPE, examined by Lindroth (1962:7), in MNP. Type locality: "Amérique septentrionale".

Bembidium lacustre LeConte, 1848:451. HOLOTYPE female, examined, in MCZ. Labeled: "[grayish-green circle] / 428 / Type 5491 [red label] / *var.* lacustre Lec. [handwritten] / Bembidion inaequale Say Det Lindroth 1951." Type locality Lake Superior, according to Lindroth (1962:7).

Bembidion opaciceps Casey, 1918:8. LECTOTYPE female designated by Lindroth, 1975:115, examined, in USNM. Labeled: "Cal. / CASEY bequest 1925 / TYPE USNM 36794 [red label] / opaciceps Csy [handwritten] / LECTOTYPE opaciceps Csy By C. H. Lindroth." Type locality California.

Derivation of Specific Epithet. From the Latin *inaequalis,* referring to the unequal surface of the elytra.

Characteristics of Adult. (Figs. 22, 23, 73, 74, 126, 142, 162, 178.)

Diagnostic combination. Mirrors present on intervals 2 through 7; outer mirrors on intervals 6 and 7 near posterior silver spots, frequently isolated from inner mirrors (Figs. 22, 23); pronotum with carina short or absent, midlateral seta present or absent; aedeagus with prominent ventral bulge and hooked apex (Fig. 126); extensive dorsal field of comb-like scales; VSP scaly, as in *B. levettei.*

Comparisons with related species. Belongs to the *B. inaequale*-subgroup. Adults are generally smaller than those of *B. levettei*, from which they differ externally by small silver spots, and the mirror on elytral intervals 6 and 7 being positioned near the posterior silver spot. Generally the outer mirror is a small spot, isolated from the inner mirrors, but in many specimens it is broadly connected to inner mirrors. Eastern members of *B. inaequale* are more readily distinguished from *B. levettei* specimens by the narrow forebody with deeply punctured striae, and pale tibia.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.3–5.9 mm. Dorsal surface ranging from dark bronze or dark aeneous to gray green, aeneous, or bluish green; mirrors dark purplish black, dark bronze, or coppery, or reddish. Antenna with first four antennomeres pale, at least basally, or more generally infuscated; tibia centrally pale, rufous or rufotestaceous with slight metallic tint; femora basally pale; western specimens with more generally infuscated legs. Faint discal shiny patch flanked by dull patches on pronotum. Pronotum varied, from convex and narrow to flat and wide. Transverse basal impression of elytra not as pronounced as in *B. levettei*, in many specimens absent; humeral margin short to medium in length, not extended to stria 5; striae slightly to markedly punctate; 5 and 6 in many specimens interrupted at outer mirror; 4 in many specimens interrupted. Spermatheca quite varied; cornu slightly curved, length varied, as short as in Figure 179 or nearly as long as in *B. levettei* (Fig. 177). Spermathecal duct without posterior lobe. Stylomeres as in Figure 162.

Characteristics of First Instar Larva. (Fig. 193.)

Diagnostic combination. As for *B. lorquinii.* LHw = 330–400 μm, LHl = 260–340 μm, LCl/LHl = 0.111–0.161. Four specimens measured. See Table 2 for complete description.

Characteristics of Second Instar Larva.

Description. As for *B. lorquinii.*

Specimens Examined. I have seen 1,802 adults, 62 first instars, 4 second instars, and 2 third instars from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DEUN, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, ISAs, JHAc, JKLi, KUSM, MCZ, OSUO, ROM, SMNH, UASM, UBC, UCB, UMSP, UMMZ, USNM, UWLW, ZIL.

Geographic Distribution. In North America from Nova Scotia, south to Georgia and Alabama, west to Kansas, Colorado, and California, north to Alaska (Fig. 273).

Geographic Variation. This species shows considerable geographic variation. Lindroth (1963) divided *B. inaequale* into two subspecies, but I do not consider them discrete enough to be recognized. Adults from east of the Great Plains ("*B. inaequale inaequale*," Fig. 22) are generally more somber in color, have paler legs, shinier luster, narrower body (especially the forebody), and deeper elytral punctures; they lack the midlateral pronotal seta. Specimens from the western mountains ("*B. inaequale opaciceps*," Fig. 23) are wider and more robust; the microsculpture is deeper, with surface therefore duller; pronotum wider with less sinuate sides and broader base; midlateral setae present in most specimens; striae much shallower, with less impressed punctures; shoulder margin a bit longer. The two forms are quite different. However, there is a broad zone of intermediates, from Alberta and Manitoba south to Colorado, Wyoming, and Nebraska. Within this intergradation zone there is also notable variation, with Alberta and Saskatchewan specimens being: larger, more reddish, with smaller silver spots, restricted to interval 3; with mirrors more extensive, outer mirrors frequently not isolated. Making the picture more complex are five specimens from Nampa, Idaho (ICCM!), which appear quite like intergrade specimens from western Nebraska, even though they are from well within the range of the western form. I feel that a detailed morphometric study of the patterns of geographic variation in this species is necessary before any clear division into subspecies is undertaken.

Habitat. Found on river, creek, and lake banks. Generally among sparse vegetation on a silt-sand substrate.

Phylogenetic Relationships. B. inaequale is either the sister species of *B. levettei levettei*, *B. levettei carrianum*, the *B. litorale-B. conicolle* line, or a combination thereof (Figs. 292, 293).

Bembidion litorale (Olivier)

Elaphrus litoralis Olivier, 1790:6. Location of type unknown, according to Lindroth (1962:6). Type locality Paris, France.

Elaphrus paludosus Panzer, 1794, number 4. Location of type unknown. Type locality Nürnberg, Germany.

Bembidium elegans Germar, 1824:27. Location of type unkown. Type area Transsylvania.

Bembidium var. *caeruleum* Krynicki, 1832:85 (not Serville, 1826:76). Type presumably in Krynicki collection, University of Charkow (Horn and Kahle, 1937). Type locality undesignated. (Name available as original description does not give clear indication that the name is intended to be infrasubspecific.)

(*Bembicidium palmosum* var. *evanescens* Dalla Torre, 1877:53 [not Wollaston, 1877:18]. Presumably "*palmosum* Pnz" is an emendation of "*paludosum* Panzer." [Name unavailable as intended as infrasubspecific.])

(*Bembidium littorale* v. *nigrans* Barthe, 1912:234. [Name unavailable as infrasubspecific, as indicated by "Ça et là avec le type." (Barthe, 1912:234).])

(*Bembidium litorale* ab. *melanoticum* Wagner, 1915: 307. [Name unavailable as intended as infrasubspecific.])

(*Bembidion litorale* ab. *krynickii* Csiki, 1928:35; new name for *Bembidium* var. *coeruleum* Krynicki, 1832. [Name not available, as Csiki considered it of infrasubspecific rank.])

B. littorale auctorum.

Derivation of Specific Epithet. From the Latin *litoralis*, meaning "of the shore," referring to the beachside habitat of these beetles.

Characteristics of Adult. (Figs. 17, 56, 81, 127, 143, 163, 179.)

Diagnostic combination. Mirrors on intervals 2 through 7, outer mirrors broadly connected or isolated from inner mirrors; pronotum basally constricted (Fig. 17), somewhat convex, lacking carina, midlateral setae present or absent; male protarsomere adhesive setae narrow (as in Fig. 86); aedeagus stout (Fig. 127), with dorsally bent ventral margin of the ostial cavity; VSP large, with unscaled (but occasionally striated) dorsal ridge; ostial microtrichial patch narrow, dense.

Comparisons with related species. Belongs to the *B. inaequale*-subgroup. Males of this species have exceptionally thin basal protarsomeres, with small adhesive setae, traits they share with members of the closely related *B. conicolle*. *B. litorale* has a more convex prothorax with more rounded sides (that is, much more basally constricted) than does *B. conicolle*. Other differences from *B. conicolle* are described under that species.

Both Netolitzky (1940, 1942) and Lindroth (1962) considered the eastern populations of *B. litorale*-like *Bracteon* to belong to a separate species, *B. conicolle*. O. L. Kryzhanovskij (pers. comm., 1983) suggests that *B. conicolle* and *B. litorale* belong to the same polytypic species. I have decided to treat the forms as distinct species, in good part because the limited material before me prevents a definitive conclusion (and thus I would prefer to err on the side of conservancy), but also because of the nature of the geographic variation. The few (11) specimens I have from a zone of sympatry, the Lena River, belong to two forms. Two females (Ust Kut, UMHF!) with convex, rounded prothorax, possessing midlateral setae, ed3 and ed5 in center of silver spots, and outer mirrors isolated, are typical *B. litorale* members. Nine specimens (Ust Aldan, Aldan, Ust Kut, Ust Vilui, UMHF!) are more similar to typical *B. conicolle*, having flatter, less rounded prothoraces, lacking midlateral setae, having ed3 and ed5 at or near the anterior edge of silver spots, and having outer mirrors broadly connected to inner mirrors or partly isolated. However, most of the characters Lindroth (1962) uses to separate the species are inconstant (especially the isolation of the outer mirrors), and the differences between the forms are rather slight. Kryzhanovskij's suggestion of synonymy of the two names thus deserves greater attention than I have been able to give it; an examination of geographic variation of *B. litorale*-like *Bracteon* based on more extensive material is warranted.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.2–5.9 mm. Dorsal surface bronze gray, bronze, or greenish gray; mirrors dark bronze gray, or purplish. Appendages dark, with venter of antennomere 1, base of legs, and venter of tibiae paler (rufous or rufopiceous). Deeply microsculptured, and therefore quite dull. Shinier specimens show a slight silver spot on the prothorax. Convex pronotum, sides distinctly rounded, greatest width well before middle; base narrow. Humeral margins of elytra short, not extended to stria 5; striae slightly to moderately impressed. Spermatheca as in Figure 179; cornu straight, basal bulb small. Spermathecal duct without posterior lobe. Stylomeres as in Figure 163.

Characteristics of First Instar Larva. Unknown.

Characteristics of Second and Third Instar Larvae.

Diagnostic combination. Described by Andersen (1966); he does not provide information on the characters I studied.

Specimens Examined. I have seen 241 adults from the following collections: AMNH, BMNH, CAS, HNHM, ICCM, MCZ, UMHF, USNM, ZMLS.

Geographic Distribution. A Palearctic species, found from the British Isles and Spain, to Greece, north to Finland, and east across Asia to the Lena River (Lindroth, 1962; Fig. 274).

Geographic Variation. None noted.

Habitat. On banks of rivers and small lakes, on fine sand often mixed with silt; bank often sparsely vegetated (Lindroth, 1945). The habitat is thus similar to that of *B. inaequale*.

Phylogenetic Relationships. B. litorale is the sister species of *B. conicolle*, or of *B. levettei* + *B. inaequale* (Figs. 292, 293).

Bembidion conicolle Motschulsky

Bembidium conicolle Motschulsky, 1845:273. LECTOTYPE female designated by Lafer (1975), examined, in ZMUM, labeled: "Mt. Hamar-Dab [red label] / Bembidium conicicolle mihi, Mt. Ham. Dab [handwritten on bordered paper] / Lectotypus Bembidion conicolle Motsch. Lafer det. [red label]." Type locality Hamar Daban Mountains, near Lake Baikal, Russia

Bembicidium conicicolle Motschulsky, 1850:16; unjustified emendation of *Bembidium conicolle* Motschulsky, 1845.

Bembidion baikalo-ussuricum Netolitzky, 1940:163. HOLOTYPE male, examined by Lindroth (1962: 7), in Naturh. Mus. Vienna. Type locality Nikolsk-Ussurisk, north of Vladivostok, Russia. For notes on synonymy, see Lafer (1975).

Bembidion baicaloussuricum auctorum.

Derivation of Specific Epithet. Presumably referring to the trapezoidal pronotum of members of this species.

Characteristics of Adult. (Figs. 18, 86, 128, 144, 164.)

Diagnostic combination. Mirrors on intervals 2 through 7, outer mirrors broadly connected or isolated from inner mirrors; pronotum only slightly basally constricted (Fig. 18), relatively flat, generally with small carina, midlateral setae present or absent; male protarsomere adhesive setae narrow; aedeagus narrower than in *B. litorale*, with less curved ostial sclerotized strip (Fig. 128); VSP large, with unscaled (but occasionally striated) dorsal ridge; ostial microtrichial patch narrow, thick.

Comparisons with related species. Belongs to the *B. inaequale*-subgroup. Very similar to specimens of *B. litorale*. The prothorax of *B. conicolle* is flatter, with straighter sides and a wider base than that of *B. litorale;* the midlateral seta is constantly absent in *B. conicolle*, only inconstantly so in *B. litorale.* A minute laterobasal carina is present in most *B. conicolle*, but in no *B. litorale*. The outer mirrors are broadly connected to the inner elytral mirrors in most, but not all, specimens. Stria 4 is generally straighter (although in some specimens it is abruptly sinuate); ed3 and ed5 are at the anterior margin of the silver spot in most specimens. Aedeagus very similar to that of *B. litorale* (compare Figs. 127 and 128); slenderer, VSP usually thinner, with anterior basin shallower, ventral margin thus appearing straighter in side view; ostial cavity without markedly bent ventral margin.

Distinguished from the North American *B. levettei* by the lack of the prothoracic seta and the narrow protarsomere of the male.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.3–5.7 mm. Stylomeres as in *B. litorale;* see Figure 164.

Characteristics of First Instar Larva. Unknown.

Specimens Examined. I have seen 21 adults from the following collections: HNHM, UMHF, ZMLS.

Geographic Distribution. From the Lena River, Lake Baikal, and Mongolian Peoples' Republic, east to the Ussur region and Japan (Fig. 274; Lindroth, 1962).

Geographic Variation. None noted.

Habitat. Not known to me.

Phylogenetic Relationships. This species is probably most closely related to *B. litorale* or to *B. levettei* + *B. inaequale* (Figs. 292, 293).

PHYLOGENY OF *BRACTEON*

Introduction

Of primary importance in deciphering the course of biotic history is the discovery of the pattern of splitting of lineages, and of the manner in which traits have been transmitted along lineages. But breeding ties of past organisms cannot be observed directly, and so some secondary indicators of genealogical relationship must be sought. The only evidence we have for a group such as *Bracteon* is that provided by the characteristics of living species; the few *Bracteon* fossils offer little information.

The hypotheses of phylogenetic branching pattern and character state evolution to be chosen for a group such as *Bracteon* are those that best explain the diversity in extant organisms. It is important that we strive to make our hypotheses of character evolution and phylogeny to be the "best explanatory hypotheses" not just in isolation but also within a broader framework. We have to consider them in the context of hypotheses about related groups and of established notions about genetics, development, evolutionary ecology, etc. For example, we must make sure that we choose hypotheses for our study group ("ingroup") that allow for "acceptable" hypotheses of related group ("outgroup") evolution; we do this by using some form of outgroup analysis. We must also make certain our hypotheses are consistent with our background assumptions about evolutionary rates, developmental constraints, etc. This striving for compatibility of our hypotheses with the rest of biological knowledge is important whatever our phylogeny reconstruction methods might be. But which background assumptions are justifiable?

Two divergent opinions form the focus of one of the most crucial controversies in systematics today: Felsenstein (1982, 1983, 1988) recommends that we choose the phylogeny that confers on the data the greatest likelihood of observation under a particular model of evolution; Farris (1983) believes we should choose the phylogeny that allows us to most simply account for the observed distribution of character states, without relying on stochastic evolutionary models. We could choose the most-parsimonious hypothesis (*sensu* Farris) either for purely aesthetic reasons (because parsimonious hypotheses are pleasing), or as they might be viewed, through their simplicity and presumed greater testability, as appropiate Popperian devices to stimulate future research, or because some stochastic model of evolution judges parsimony to be a good estimator of phylogeny (see Sober, 1988). A number of different stochastic models might so judge parsimony, but these have only been partially explored (Felsenstein, 1988), and all of the models examined to date are to greater or lesser extent biologically unrealistic. The same can be said of any particular maximum likelihood method. We are therefore left in the uncomfortable position of using a method which could be justified if the characters studied evolve according to some realistic, but unknown, model.

For morphological data such as that available for *Bracteon*, I have no clearly defensible stochastic models of character evolution that would allow us to build statistical estimation methods. My algorithmic analysis will therefore be based on parsimony methods.

Before delving into the phylogeny of *Bracteon* and its near relatives, I will discuss briefly its more distant relatives.

The Phylogenetic Context of *Bracteon*

Suprageneric Relationships within the Supertribe Trechitae. While relationships of major lineages of Trechitae are not crucial for my study of *Bracteon*, they provide a useful context within which to consider the evolution of *Bracteon* and its near relatives. Below I review a few aspects of trechites, concentrating on the tribe Bembidiini.

Four tribes are included within the supertribe: Trechini, Zolini, Pogonini, and Bembidiini (Kryzhanovskij, 1976; Erwin, 1985). Virtually no cladistic studies on the higher-level relationships of the members of these tribes have been published. Erwin's (1972, 1982) papers are the only available works, and these only deal with a very few aspects of bembidiine phylogeny. Other studies include Jeannel (1941), Barr (1971), Schuler (1971), and Perrault (1981), but the character analysis in these is somewhat vague or not explicit. A complete analysis of major evolutionary patterns within trechites is far beyond the scope of the present work.

Figure 275 presents some names of major groups of trechites, and hypotheses of some possible aspects of their phylogeny; it is based mainly on the previously cited works. The meager cladistic structure illustrated in the figure is in doubt: the monophyly of the groups shown, and their relationships, have not been adequately demonstrated.

Monophyly of Bembidiini. The tribe Bembidiini includes thousands of species of carabids with small or minute adults, which occur throughout the world. The only known derived character linking members of the Bembidiini are the subconical, narrow, and short apical palpomeres (Erwin, 1982). However, some trechines (for example, *Oxytrechus* Jeannel and *Perileptus* Schaum) also have relatively small terminal palpomeres. A bembidiine-like palpus occurs as well in the aberrant genus *Gehringia* Darlington, a genus with doubtful affinities to bembidiines (D. Maddison, 1985a). There is some uncertainty about the nature of palpomere evolution, and thus about bembidiine monophyly; the character needs to be studied in more detail.

Generic Relationships within Bembidiini. Members of the tribe containing *Bembidion* are organized by some workers into the three subtribes Anillina, Tachyina, and Bembidiina. All are worldwide groups, with the small tachyines being predominantly tropical, the larger bembidiines mainly temperate, and the minute, soil-dwelling anillines occurring in unglaciated regions.

Erwin (1982) proposes that Anillina is a polyphyletic grade derived from the tachyine *Paratachys* Casey and its allies. *Limnastis* Motschulsky and relatives, plus *Horologion* Valentine are also presumably derived from this same group (Barr, 1971; Erwin, 1982).

Among Bembidiina, Erwin (1972) considers *Asaphidion* and *Bembidion* to be sister groups, indicated by common possession of the (presumably derived) brush on male internal sacs. This character state is not found in other Bembidiina, but it is found as well in the tachyine *Xystosomus* Schaum (Erwin, 1973). Another genus of doubtful affinities is the Australian *Tasmanitachoides* Erwin, now placed in the Tachyina (Erwin, 1972). *Phrypeus* is considered by Erwin (1972) to be the sister group of *Asaphidion* + *Bembidion*, with *Bembidarenas* being the sister group of that whole assemblage. Erwin does not treat *Zecillenus*, but in this scheme it would presumably fall outside of the *Asaphidion* + *Bembidion* group because of its supposedly primitive lack of a brush sclerite. Perrault (1981), in contrast, considers the lack of a brush sclerite in *Bembidarenas* and *Phrypeus* (and presumably *Zecillenus*) to be derived, and would include these within *Bembidion* (sens. lat.). A more certain sorting of these genera awaits extensive character analysis, including study of promising characters such as male protarsal vestiture, testicular structure, etc.

Monophyly of Bembidion. The only character typically cited (Erwin, 1972; Lindroth, 1980) linking *Bembidion* members is the brush sclerite of the male internal sac (Figs. 99–102, 107). However, *Asaphidion* and *Xystosomus* also possess such a brush, and thus it cannot be considered an autapomorphy of *Bembidion* as the genus now stands. I know of no other possible synapomorphy of members of the genus, and *Bembidion* may be paraphyletic or polyphyletic, with one or more of the less-inclusive genera of Bembidiina derived from within it.

Cladistic Structure of *Bracteon* and Related *Bembidion*

No cladistic analysis of relationships of subgenera of *Bembidion* has been published. Erwin and Kavanaugh (1981) present the only available cladistic analysis of members of the genus, but they deal with relationships within two species groups only, distantly related to *Bracteon*.

The main attempt at tracing lineages within the genus was made by Jeannel (1941), with modifications of his scheme proposed by Perrault (1981, 1982). These works, however, did not include a cladistic character analysis. Jeannel (1941) lists seven phylogenetic series within the French bembidiine fauna: *Ocys, Cillenus, Notaphus, Bembidion, Peryphus, Odontium,* and *Asaphidion*. Based on the South American fauna, Jeannel (1962) later removed *Plataphus* from the *Peryphus* series. He does not discuss the interrelationships of these eight series.

Netolitzky (1942), in contrast, distinguished two major phyletic series in his studies of *Bembidion*, the *Notaphus* series (with "free" ed3 and ed5), and the *Peryphus* series (with ed3 and ed5 attached to stria). He presents a number of other series of evolving lines (based on changes in form of mentum tooth, humeral margin, etc.) interwoven with these two series, but the discussion is lacking clear hypotheses of relationships of taxa.

Perrault (1982) also views *Bembidion* as comprising two major lineages, but of different compositions than Netolitzky's. According to Perrault, *Bembidion* originated in the tropics, with an ancient separation of two stocks leading to the eastern Southern Hemisphere forms on one hand, and to the speciose Northern Hemisphere and South American taxa on the other.

In my opinion, none of these views have been corroborated, and at present must be considered very tentative working hypotheses.

I herein present a first attempt at a cladistic analysis of *Bembidion*, including 52 taxa from a number of subgenera, with hopes that this initial contribution will serve as a starting point for future phylogenetic studies in the genus. Because my main interest is with *Bracteon*, most of my effort is placed there.

Methods

I have examined 85 traits in the 18 taxa of *Bracteon*, 38 other *Bembidion*, as well as *Asaphidion alaskanum* (Tables 2, 4, and 5). I thus have 18 taxa in my study group (ingroup), and 39 outgroup taxa. Some of the characters (for example, 10, 26, 28, and

32) have been used in the past to group *Bembidion* into subgenera or species-groups; others vary only within the outgroups, and are constant within *Bracteon*. These are included primarily for the evidence they might offer regarding outgroup relationships. Table 3 presents the number of specimens examined for each entry in Table 2; sample sizes for Tables 4 and 5 are contained therein.

I have conducted an analysis using traditional Hennigian argumentation, not employing a computer (which I will call the "traditional analysis"), as well as a computer-aided, fully algorithmic parsimony analysis of these data (which I will call the "algorithmic analysis"). Before going into details about each analysis, I describe the gathering and weighing of evidence.

Choice of characters

In choosing evidence for my cladistic analysis, I have discarded about 50 characters after preliminary investigation. Characters eliminated were those that proved: (1) to be too difficult to interpret states of a given specimen without resorting to expensive SEM or other excessively time-consuming work; (2) to have too much variation within species, requiring much more time to document accurately than was available. I also avoided characters that required extensive measurements. While some of the characters used are inherently quantitative (such as length of some larval setae), the organisms exhibit discrete conditions that could readily be distinguished by eye. After this pruning, 85 characters remained.

Hypothesizing transformation networks

For each character, all changes between states were equally weighted, with one major exception. All multistate characters whose traits were considered as ordered in a transformation series were treated as linearly ordered, reversible characters. Thus, a character ordered into a 0↔1↔2 transformation series implies that a 0↔2 change is of greater weight than a 0↔1 change. The only multistate characters not fitting into this category were characters 34 and 64, which were treated as unordered characters.

Character weighting

Initial analyses were conducted with equal weighting of characters. I should note that this equality of inter-character weighting is somewhat artificial, as some of the characters are weighted more than others simply by the way I coded the characters. I divided some characters into two states (say 0 and 1), others into three (say A, B, and C); the characters with more states are naturally weighted more highly than the ones with less, but this does not necessarily reflect greater genetic diversity requiring higher weights. Without knowing considerably more about *Bembidion*, it is not possible to determine whether the genetic distance between 0 and 1 is any more or less than that between A and B or A and C. However, in the face of ignorance, I think that this (somewhat questionable) equality of weights is the best that can be done.

Two additional weighting schemes were explored. In the first, I weighted against all characters that were subject to observational error, that is, I doubted I could distinguish character states consistently, or I felt the sample sizes were too small. In this weighting scheme, error-prone characters were given a weight of 1, other characters a weight of 2. The characters I judged to be error-prone are: 8, 11, 15, 16, 27, 28, 32, 35–38, 40, 45, 46, 51, 60, 64, 70, 73, 82, 83. In the second, I weighted against error-prone characters, as well as those that were polymorphic in at least two species. The relative decrease in weight is based on the assumption that polymorphisms which are maintained are less reliable phylogenetic indicators (see Kluge and Farris, 1969; Hecht and Edwards, 1976). In addition, the numerical algorithms used for dealing with polymorphic data are biologically unrealistic (they do not allow for ancestral polymorphisms), thus leaving the treatment of such characters questionable. By this weighting scheme, characters that were both error-prone and overly polymorphic were given a weight of 1, those that suffered from only one problem a weight of 2, and all other characters a weight of 3. The characters which show polymorphism in two or more species are: 3–11, 21, 25 27–29, 35, 40, 45–46, 51, 57, 60, 75, and 82.

Traditional analysis

Many of the non-numerical approaches used by systematists are essentially less-rigorous versions of maximum likelihood estimation, or a parsimony approach, or an amalgam of the two. The rigorous portions of these mental techniques are by necessity shorter and less complex than those used in computers, and, as expected, they are therefore less powerful. The non-rigorous portions make up for some of this lack of depth by allowing inclusion of more information in the analysis. However, these non-rigorous, more intuitive portions of the method lack openness to critical examination. (The hypotheses they produce are open to critical examination, as are all hypotheses, but the methods are not.)

Of the non-numerical methods currently used for inferring the phylogeny of a group of organisms, almost all involve an initial assessment as to which states of a character were present in an ancestor of the ingroup. Methods proposed for inferring which states are ancestral (or which derived) are numerous, and have been reviewed by Crisci and Stuessy (1980), de Jong (1980), Stevens (1980), Arnold (1981), and others. The three methods most widely discussed today are outgroup analysis, the ontogenetic method, and the paleontologic method. The debate in the literature on the relative merits of these techniques, carried on by Nelson (1978), Patterson (1982), Voorzanger and van der Steen (1982), and W. Maddison *et al.* (1984), among many others, is unfortunately nearly irrelevant for ground beetle systematics: the ontogeny and fossil record of carabids, including *Bracteon*, are so poorly known that these methods are for the most part inapplicable; only outgroup analysis is available.

A number of outgroup analysis procedures have been proposed (see Watrous and Wheeler, 1981; W. Maddison *et al.*, 1984). When outgroups are adequately resolved cladistically, the character states of the most recent common ancestor of the ingroup plus its sister group are estimated via an outgroup algorithm (W. Maddison *et al.*, 1984), and then a second step of resolving the ingroup assuming those ancestral states is taken.

These hypotheses of ancestral state can then be used to corroborate the monophyly of subgroups that possess derived states (Hennig, 1966). Two steps are thus involved: initial hypothesizing of ancestral states, and resolution of the ingroup. Rigorous techniques of argument for this second step are more or less undeveloped, although Watrous and Wheeler's (1981) functional outgroup/functional ingroup routine (equivalent to Kavanaugh's [1978] "character correlation" method and Clark's [1978] "ingroup analysis") is a useful, albeit imperfect, method of searching for most-parsimonious trees (see W. Maddison *et al.*, 1984 for a discussion of some of its problems).

However, when outgroups are imprecisely resolved, the outgroups and ingroups must be resolved simultaneously to guarantee the globally most-parsimonious ingroup cladogram. One could imagine doing this mentally, by a reciprocal illumination technique that would entail resolution of part of the ingroup, then part of the outgroup, then a portion of the ingroup, and so on, until all the data provided by the characters were used. Such a technique has not been rigorously developed, and even if it were, it would probably suffer from some of the same problems as the functional outgroup/functional ingroup approach. Nonetheless, it may be the best we could do without lengthy calculations best done by a computer. Further discussion of the relationship between techniques of argument and the globally most-parsimonious cladogram is given by W. Maddison *et al.* (1984).

The use of the outgroup analysis procedure of W. Maddison *et al.* (1984) followed by a traditional, non-numerical ingroup resolution procedure could encompass a search for the most-parsimonious tree. It might thus seem to be simply a non-numerical version of computerized parsimony analysis, with less hope of successfully finding the most-parsimonious tree. However, it does have the advantage over available most-parsimonious-tree searching programs in that the systematist is likely to subconsciously include in the analysis data not incorporated in an algorithmic analysis, data acquired over years of examining the organisms.

I will briefly outline my traditional analysis; a more complete, step-by-step description of the analysis can be found in D. Maddison (1985c). To begin the traditional analysis, I first used some of the characters listed in Tables 2, 4, and 5 to infer a few aspects of the cladistic structure of *Bembidion* (Fig. 276).

I then chose, as ancestral to *Bracteon*, a state that allows for a simple hypothesis of outgroup evolution, using the outgroup algorithm of W. Maddison *et al.* (1984). This procedure was complicated by the fact that the relationships were uncertain for *Bracteon* outgroups (Fig. 276), and so the algorithm could not be applied directly. This uncertainty in outgroup structure reflects the large number of possible resolutions of relationships. For this study the number of possible full resolutions of near-outgroup (*Pseudoperyphus* + *Odontium* subgeneric-group) structure shown in Figure 276 is 1.9 trillion (see Felsenstein, 1978). The outgroup algorithm could be applied to each possible resolution, and for each a set of possible ancestral state assessments could be obtained; but this would be dreadfully time-consuming. Fortunately, for some characters the outgroup uncertainties are irrelevant for the outgroup analysis, and an unequivocal ancestral state assessment is produced; this occurs when all possible resolutions yield the same most-parsimonious hypothesis of ancestral state (for example, if the character is invariant among the outgroups). But for most characters, different outgroup resolutions will yield different assessments of ancestral state. For these characters, I determined as many distinct assignments of ancestral states as possible, by inspection of the tree and distribution of states. Consider, for example, character 2. If *B. americanum* is the sister group of *B. bifossulatum*, and *Ochthedromus* the sister group of *Bracteon*, with (*B. chloropus* + *B. fusiforme*) + *B. aeneipes* the next-most distant sister group, then the ancestral state assessment for *Bracteon* is state 2 (slight mirrors present). If, however, *B. durangoense* is the sister group of *Bracteon*, with *B. robusticolle* next down the line, then state 0 is the assessment. Another arrangement of outgroups would yield state 1; no arrangements would yield state 3. Thus the set of possible ancestral state assessments is {0, 1, 2}. Other characters were treated similarly. For each, I condensed outgroup information, recording the range of preferred ancestral states. Taking these into account will at least partly allow for simple hypotheses of outgroup evolution. It is not an ideal technique, as character interactions are not taken into account (W. Maddison *et al.*, 1984).

The next step in the analysis is the deciphering of lineages within *Bracteon*. Not all 85 characters are useful for this. Fifteen of the characters are invariant within *Bracteon;* these include some of the characters that were used to infer outgroup relationships shown in Figure 276. As well, outgroup analysis indicated that in over 20 of the 70 remaining characters, the outgroup information at hand provided no initial clue as to ancestral states of *Bracteon*. The assessments of ancestral states for the remaining characters lead to hypotheses of derived states within *Bracteon* plus its stem group. Seventeen of these characters showed only states autapomorphic for single species, and thus they provide no evidence for joining species together. The remaining 30 or so characters form the basis for the next step of the analysis. To infer clades within *Bracteon*, I attempted to find a phylogeny that would be as consistent as possible with a monophyletic origin of each set of species sharing derived characters; that is, I tried to propose as few origins of derived states as possible. I further refined the phylogeny by then incorporating information from all of the other characters. A multistep procedure was used, with cladistic structure slowly being built up, this cladistic structure then allowing me to begin to understand evolution in the initially uninterpretable characters. The procedure used was thus similar to Watrous and Wheeler's (1981) functional outgroup/functional ingroup method. I cannot describe it more explicitly, as it was not done rigorously.

I then reexamined this initial cladogram and tried to improve it by mentally rearranging some of the branches. The resulting phylogeny is presented in Figure 277. Because of conflicting evidence, I was most uncertain about the placement of *B. punctatostriatum*, and, to a lesser extent, *B. stenoderum* and *B. carinula*.

Algorithmic analysis

After the traditional analysis was completed, most-parsimonious trees were searched for by the computer program PAUP versions 3.0q and 3.0s (Swofford, 1991). A few searches were also made by Hennig86 version 1.5 (Farris, 1988). In the PAUP analyses several terminal taxa were coded as polymorphic, and steps within polymorphic terminal taxa are added to the treelength. As Hennig86 cannot accept polymorphic terminal taxa, all polymorphic terminal taxa were recoded for ordered characters using additive binary recoding. This has the effect of treating the multistate taxa as having uncertain state, rather than polymorphisms, but this does not affect relative treelengths, and thus does not affect judging the parsimony of a tree.

The trees discovered were analyzed using MacClade version 3.0 (Maddison and Maddison, 1992). MacClade's Compare Two Tree Files facility was used to determine those characters that consistently supported one set of trees over another set of trees. MacClade was also used to determine branch lengths and examine character evolution. The data matrix is included on computer disk with version 3.0 of MacClade, or it can be requested from the author.

Four searches were conducted on a restricted set of taxa (only the 18 *Bracteon* taxa, or *Bracteon* plus *B. striatum*). The characters were either equally weighted or error-prone characters were weighted against (see "Character Weighting," above). PAUP's branch and bound searching was used to guarantee discovery of the shortest trees. Strict consensus trees of the trees resulting from these 4 searches are shown in Figures 278–281.

The remaining searches were conducted on the full set of taxa from Tables 2, 4, and 5, excluding *B. scopulinum*, *B. obscurellum*, *B. petrosum*, and *B. "kuprianovi-#1."* These four outgroup species were removed because preliminary searches with PAUP indicated that slight rearrangements among them were vastly inflating the number of equally parsimonious trees, thus significantly impairing the searches for short trees. This probably would not have much impact on inferred *Bracteon* phylogeny, as in this preliminary search these taxa were well removed from *Bracteon*, and were clustered down near the base of *Bembidion*. All PAUP searches on the set of 53 taxa were conducted using tree-bisection-reconnection (TBR) branch rearranging, with MAXTREES set to 1,000, STEEPEST DESCENT turned off, and zero-length branches collapsed. For some runs, the CHUCK option was used with CHUCKLEN set to 1 greater than the length of the shortest trees and NCHUCK set to 40. For each set of character weights, multiple searches were conducted, each beginning with a tree built by a random addition sequence. Five Hennig86 searches were conducted, beginning with the different starting points provided by mhennig, mhennig*, hennig, hennig*, and tread (the latter providing a bush). Each of these were given to the branch rearranger, bb*.

Characters 5, 6, 11, 45, 46, and 48 in the data matrix are inapplicable for some taxa. For example, those taxa without an ostial sclerotized strip (character 47), cannot be said to have a beaded or unbeaded strip (character 48). This is indicated by a "—" in the entries for those taxa in Tables 2, 4, and 5. In the algorithmic analysis, these entries were treated as missing data. Since the analyses were completed in 1989, the dangers of treating inapplicable entries as missing data have come to light (Platnick *et al.*, 1991; Nixon and Davis, 1991; W. Maddison, in press). A preliminary reanalysis was done to study the effect of treating inapplicable entries as missing data, and is described below, under "Recoded data matrix, equal weights." All other analyses examined the unrecoded matrix.

I will first describe the results of three analyses with the unrecoded matrix. These analyses differ in the relative weights applied to characters. After a description of the analysis on the recoded matrix, I present a summary of all numerical analyses. For the trees found, the treelength, consistency index, and retention index (Archie, 1989; Farris, 1989) are given.

Full Data Matrix, Equal Weights. In total, 545 equally parsimonious trees were found by PAUP in 1,167 searches, including 224 trees that were also found by Hennig86. All were of length 653, with a consistency index of 0.490, and a retention index of 0.643.

There was variation among the different PAUP searches in the collection of most-parsimonious trees discovered. For example, one search produced a collection of 84 trees, all of which were rather similar one to another, but which differed from the collections of trees found by some other searches. The collection of trees resulting from a single search is one "island" of trees (D. Maddison, 1991). In total this data matrix yields 12 islands of most-parsimonious trees, with 1, 8, 12, 12, 32, 36, 40, 44, 48, 68, 84, and 160 trees respectively, for a total of 545 trees. In the 1,167 searches conducted, each island was found more than once, with the island of 32 trees encountered most rarely (in 10 searches) and the island of 84 trees encountered most frequently (in 192 searches).

The strict consensus tree of the 545 trees, shown in Figure 282, is relatively unresolved. However, this does not mean that the 545 trees are all very different from one another, as there are only 5 distinct sorts of trees. One hundred and forty of the trees, comprising all of 3 islands and parts of 3 others, have *Bracteon* as a clade (Fig. 283). Eighty-eight of the trees in 3 islands have *B. balli* and *B. foveum* excluded from *Bracteon*, with *B. striatum* the sister group of the rest of *Bracteon* (Fig. 284). Two hundred and sixty-eight trees in 4 islands have the clade containing *B. argenteolum*, *B. alaskense*, and *B. semenovi* far removed from the rest of *Bracteon*, and placed within the complex of North American and East Asian *Odontium* related to *B. aenulum* and *B. fusiforme* (Fig. 285). Forty-eight trees in one island have a similar arrangement, but with *B. stenoderum* also included with the *B. argenteolum* clade (Fig. 286). A single tree (Fig. 287), the only member of an island, itself isolated in an island of 82 trees of length 654, has *Bracteon* shattered into 3 clades, with 7 species including *B. argenteolum* and *B. velox* contained within the *B. aenulum*–*B. fusiforme* clade, *B. punctatostriatum* the sister of *Ochthedromus*, and the rest of *Bracteon* the sister of *B. persimile* + *B. foraminosum*.

Ideally, trees close to the most parsimonious should also be examined. For this data set, there are many thousands of trees of length 654. Most of these result from slight rearrangements on the structure of outgroups; these slight rearrangements do not yield significantly longer trees because of the relatively small number of characters included in the analysis that provide evidence about outgroup structure. A tree of length 654 is of interest if some characters prefer it over trees of length 653, but a tree of length 654 that only differs from a 653 tree in that it violates the evidence provided by one character is of lesser interest. Many of the trees of length 654 fall into the latter category. The vast numbers of trees in the latter category make it impractical to examine all trees of length 654. I have therefore confined my analysis to most-parsimonious trees.

While many trees just slightly longer than 653 steps exist for this data set, the vast majority of trees are much longer. I used PAUP to count the length of a random sample of 1,000,000 trees (each tree equiprobable) (Fig. 288). The shortest tree sampled was of length 980, the longest 1,178; the mean treelength is 1,107. As the longest conceivable tree for this data set is less than or equal to 1237 (the length of a bush of a "hard polytomy" [W. Maddison, 1989]), and the shortest known tree 653, the vast majority of possible trees are in a narrow range near the top of the scale, far above the observed shortest tree. This is also indicated by the value of the g_1 statistic, which, at −0.36, indicates a treelength distribution significantly more skewed than one would expect if the data contained no phylogenetic structure (Hillis and Huelsenbeck, 1992).

If the PAUP search is constrained to conform to the basic structure inferred by my traditional analysis, the shortest trees it could find in 171 searches was 657, 4 steps longer than the shortest trees. Two hundred and seventy-three such trees were found, in 4 islands.

Error-prone Characters Relatively Devalued. Five hundred PAUP searches yielded two islands (one found 33 times, the other found 49 times), totalling 120 trees of length 1,086, consistency index of 0.513, and retention index of 0.651 (Fig. 289); these trees place the 3 species around *B. argenteolum* outside of *Bracteon*, and are very similar to one of the classes of trees found in the equal weighting analysis. Sixty-eight searches by PAUP, enforcing the constraint that *Bracteon* is monophyletic, yielded 4 trees of length 1,088 (in one island that was found 10 times); thus, the shortest tree maintaining *Bracteon* as a clade is 2 steps longer than the shortest known tree. Under equal weighting, these 4 trees are among the most-parsimonious trees; they are part of the island of 44 trees of length 653. A portion of one of these four trees is presented in Figures 294–296. No Hennig86 search was conducted.

Error-prone and Polymorphic Characters Relatively Devalued. Nine hundred and sixty-three searches in PAUP yielded two islands (one found 18 times, one found 64 times), totalling 21 trees of length 1,406, consistency index of 0.484, and retention index of 0.647 (Fig. 290). These trees are very similar to those inferred under the previous weighting scheme; in fact, there are 9 trees in common. Two hundred searches by PAUP, enforcing the constraint that *Bracteon* is monophyletic, yielded 50 trees of length 1,407, in two islands (each found 10 times); thus, the shortest tree maintaining *Bracteon* as a clade is one step longer than the shortest known tree (4 of these trees are the same trees found with only error-prone characters devalued). Five Hennig86 searches, using the same options as those used for the equal weighting analysis, yielded in total 33 trees of length 1,407, with 24 of those showing *Bracteon* monophyletic.

Recoded Data Matrix, Equal Weights. To study possible problems in these analyses caused by treating inapplicable characters as missing data, an analysis was conducted on a recoded data matrix.

In recoding the matrix, each set of dependent characters was combined into one character. For example, character 48, having a beaded or unbeaded ostial sclerotized strip, is not applicable to beetles without an ostial sclerotized strip (character 47). In combining these two characters into one, larger, multistate character whose states are the absence of a strip, the presence of an unbeaded strip, or the presence of a beaded strip, the problems caused by the dependencies between the separate characters can be avoided.

For this matrix, the sets of dependent characters were combined as follows. Characters 1, 6, and 11 were fused into a character with five states: 0 = silver spots absent; 1 = silver spots present, restricted to third interval, contained setae near anterior end; 2 = silver spots present, restricted to third interval, contained seta centrally located; 3 = silver spots present, extended into fourth interval, contained setae near anterior end; 4 = silver spots present, extended into fourth interval, contained setae centrally located. A step matrix (Maddison and Maddison, 1992) was built and applied to this combined character in the analysis. It was presumed that it was one step to gain or loose a restricted silver spot, one step to extend the silver spot onto the fourth interval, and one step to change the position of the setae. Characters 4 and 5 were fused into an ordered character with five states: 0 = mirrors on intervals 6 or 7 absent; 1 = intervals 6 or 7 slightly shinier; 2 = intervals 6 or 7 with slight mirrors; 3 = interval 7 with distinct, isolated mirror; 4 = interval 7 with distinct mirror continuous with inner mirrors. Characters 44, 45, and 46 were combined into a character with 11 states: 0 = ostial microtrichial patch absent; 1 = patch small, without scales; 2 = patch medium, without scales; 3 = patch medium, with few comb-like scales; 4 = patch medium, with extensive scales; 5 = patch medium-large, without scales; 6 = patch medium-large, with few comb-like scales; 7 = patch large, without scales; 8 = patch large, with few comb-like scales; 9 = patch large, with extensive scales; 10 = patch large, with extensive scales that are sparse and small. The step matrix applied to this character presumes that it is one step to gain a small ostial microtrichial patch with no scales, one step with each increase in size of the patch or increase in the extent of scales, and one step between states 9 and 10. Characters 47 and 48 were combined into a three-state unordered character: 0 = ostial sclerotized strip absent; 1 = ostial sclerotized strip present, without beaded texture; 2 = ostial sclerotized strip present, with beaded texture.

For this recoded matrix, the length of the 545 trees found in the initial algorithmic analysis varied from 650 to 652. These treelengths are as calculated by PAUP, which does not include the steps within two polymorphic taxa (*B. inaequale* and *B. litorale*) for the character formed by the merger of characters 1, 6 and 11. MacClade includes some of these steps, and reports treelengths of 652 to 654. Treelengths will be reported using PAUP's calculations.

Most-parsimonious trees for this recoded matrix were searched in two ways. First, 100 searches were conducted with starting trees produced using random addition sequences, and subsequent TBR branch rearrangements, with NCHUCK set to 25, and CHUCKLEN set to 651. These searches yielded two islands of trees of length 650. The first island contained 44 trees, and was found five times; the second island contained 5,482 trees, and was found six times. Second, 12 searches were conducted, using as starting trees each of the 12 islands of trees found in the algorithmic analysis of the unrecoded matrix, again using TBR branch rearrangements. Three of these searches produced the same island of 44 trees of length 650, with the remaining searches finding various islands of trees of length 651.

The trees found in this preliminary analysis of the recoded matrix do not dramatically alter the conclusions drawn from the previous analyses. The island of 44 trees contained the same trees as island-44 in the unrecoded data matrix, including the tree partially shown in Figures 294–296.

These trees are included within the trees whose consensus is depicted in Figure 283, and show a monophyletic *Bracteon*. Thus, both unweighted analyses suggest the possibility of a monophyletic *Bracteon*. Trees in the island of 5,482 trees showed a novel pattern: *Ochthedromus* is split in two, with the two *B. bifossulatum* subspecies moving within *Bracteon* (Fig. 291). The diversity present among the 5,482 trees is mostly within the outgroups, as there are only 48 distinct relationships among *Bracteon* plus *B. bifossulatum* exhibited among these trees. This results in the relatively well-resolved ingroup relationships shown in Figure 291. For the unrecoded matrix, these trees are one step longer than the most parsimonious. Thus, among most-parsimonious trees without a monophyletic *Bracteon*, recoding the matrix tipped the balance slightly to favor trees with *B. bifossulatum* contained within *Bracteon*, in contrast to the trees for the unrecoded matrix, which show pieces of *Bracteon* scattered among *Odontium* and *Ochthedromus*. It should be noted, however, that this analysis does not include one of the characters that supports the monophyly of *Ochthedromus*, that is, the presence of about 10 long setae on the submentum of *Ochthedromus* adults. If this character were included, then the 5,482 trees would not be among the most parsimonious.

Discussion

Traditional versus Algorithmic Analyses. Two taxa judged to be of uncertain relationships in the traditional analysis, *B. stenoderum* and *B. punctatostriatum*, were placed in different places in the two studies. In the traditional analysis, *B. stenoderum* was placed in the *B. argenteolum* group; in the algorithmic analysis, it was placed within the *B. carinula-B. velox-B. lapponicum* clade, except for the one island in the unweighted analysis which placed *B. stenoderum* with the *B. argenteolum* group, but outside of *Bracteon* proper. *B. punctatostriatum* was placed, in all shortest trees, with weighted and unweighted characters, as sister to the *B. carinula-B. velox-B. lapponicum* clade, except for one single tree (Fig. 287) which places it as the sister to *Ochthedromus*.

Using MacClade's Compare Two Tree Files chart, I compared all 545 most-parsimonious trees, with the 273 trees of length 657 that preserves the structure inferred from the traditional analysis. All traditional analysis trees differ from all most-parsimonious trees in requiring at least one extra step in larval characters 73 (ME_2 length) and 75 (TE_6 length). Examination of the tracings of evolution of these two characters provided by MacClade indicates that the placement in Figure 277 of *B. punctatostriatum* outside of the *B. carinula-B. velox-B. lapponicum* clade, with which it shares shorter ME_2 and TE_6 setae, is the reason for this difference. Of course, these two characters only account for 2 of the 4 steps by which the traditional analysis trees differ from the most-parsimonious trees. Other combinations of characters must account for the other 2 steps.

However, allowing *B. punctatostriatum* to join the *B. carinula-B. velox-B. lapponicum* clade, but maintaining the rest of the structure in Figure 277, does not help. The shortest trees found under this constraint were again of length 657. The only character in which these trees are consistently longer than the most parsimonious is character 25 (pronotal carina shape and size). While placing *B. punctatostriatum* with *B. carinula* and relatives is supported by characters 73 and 75, the decrease in number of steps of these two characters is evidently balanced by an increase in number of steps of other characters.

The extra length present in these trees consistent with the traditional analysis is a result of the differing placement of *B. punctatostriatum*, *B. stenoderum* and relatives, not in the outgroup structure. That the outgroup structure presumed in the traditional analysis is not the constraint causing less-than-most-parsimonious trees can be seen by PAUP searches in which the outgroup structure was constrained as in Figure 277, but the ingroup was not constrained. Such searches yielded 4 trees of length 653, indicating that the problem was not solely in the outgroup structure.

Other than these relative minor differences between placement of *B. punctatostriatum, B. stenoderum* and relatives, the traditional and algorithmic analyses inferred the same basic structure of *Bracteon,* except for one profound difference: the shattering of *Bracteon* into 2 or 3 clades in some of the equal weighted trees, and all of the most-parsimonious trees under unequal weighting.

Is Bracteon *Monophyletic?* Two characters suggest that *Bracteon* is monophyletic. One derived state possibly linking *Bracteon* is the presence of elytral silver spots around ed3 and ed5. Some near-outgroup species also have the elytral surface around ed3 and ed5 modified, but in different ways from *Bracteon.* For example, *Ochthedromus* and *B. (Odontium) foraminosum* specimens have the region around ed3 and ed5 foveolate. In *B. foraminosum* the microsculpture is distinctly modified around the setae, with the sculpticells stretched. However, no distinct, granulate silver spots are present in either group. Another trait, perhaps associated with the development of the silver spots, is the movement of elytral setae ed3 and ed5 into the middle of interval in *Bracteon,* not attached to the stria. In all trees found in which *Bracteon* was not monophyletic, these two characters (numbers 1 and 10) exhibit more evolutionary steps than in the trees found in which *Bracteon* is monophyletic; these are the only characters that exhibit this pattern.

Several characters, however, speak against the monophyly of *Bracteon.* Using MacClade's Compare Two Tree Files chart, I have analyzed the characters that support shattering of *Bracteon* into two or more clades, by comparing those trees that maintain the subgenus as monophyletic with others that don't. There are three kinds of trees with shattered *Bracteon* that need to be examined.

Trees with *B. balli* and *B. foveum* separate from the rest of *Bracteon* are not consistently better for any particular character than are the trees with *Bracteon* intact. Presumably a combination of characters that favor the trees with *B. balli* and *B. foveum* removed from *Bracteon* compensate for the increased length in characters 1 and 10.

Trees with the *B. argenteolum-alaskense-semenovi* clade (with or without *B. stenoderum*) removed from *Bracteon* were among the most-parsimonious trees found under equal weighting, and formed the entire collection of most-parsimonious trees under the other two weighting schemes investigated. In all cases, these trees were favored over trees with *Bracteon* intact by characters 9 (midlateral pronotal seta), 27 (elytral basal impression), 60 (Y chromosome size), and 63 (frontale microsculpture behind FR_3). In the trees found when error-prone characters were devalued, two or more other larval characters also supported the shattered *Bracteon,* including character 65 and character 61 or 64. By placing the *B. argenteolum-alaskense-semenovi* clade within the *B. aenulum-B. fusiforme* complex, all of which lack a midlateral pronotal seta, the explanation of evolution of this trait becomes simpler. The *B. argenteolum-alaskense-semenovi* clade lacks the basal impression on the elytra characteristic of most *Bracteon.* The small Y-chromosomes of *B. alaskense* are shared among *Bracteon* only with *B. carinula;* removal of *B. alaskense* and related species from *Bracteon* is thus suggested by this trait. Finally, in characters 63 and 65, the lack of microsculpture at the back of the frontale in first instar larvae, as well as the large eggbursters, both suggest relationship to *B. aenulum.*

The odd tree of Figure 287 was supported over those of Figure 283 primarily on the basis of a large number of larval characters (61–63, 65, 66, 70).

Are these characters that speak against a monophyletic *Bracteon* good evidence of relationship? The lability of larval characters is not well known in carabids. However, it is clear that midlateral pronotal setae are quite labile, being lost frequently in carabids (note that three of the *Bembidion* species examined are polymorphic for this trait; see also Darlington, 1971b). If this untrustworthy character were omitted from the analysis, the balance would be tipped in favor of *Bracteon* monophyly. This, plus the fact that the silver spots exhibited by all *Bracteon* are unique within carabids, leads me to (tentatively) prefer the hypothesis that *Bracteon* is monophyletic.

Bold and Cautious Hypotheses. I choose to present both bold and cautious hypotheses of *Bracteon* phylogeny, in order to dispel acceptance of a single hypothesis. Weakly supported hypotheses, presented in the name of Popperian science as hypotheses to test, can be carelessly transformed through the literature into confidently accepted notions.

A relatively bold hypothesis of *Bracteon* relationships is shown in Figure 292. This figure summarizes the common elements in those trees among the most-parsimonious trees (with equal weighting) that show *Bracteon* monophyletic, as well as the most-parsimonious trees (under the two other weighting schemes, and under equal weighting of the recoded matrix) with the constraint that *Bracteon* is monophyletic. Note that it is also consistent with those trees inferred with one or no outgroups considered (Figs. 278–281). This indicates that, except for the shattering of *Bracteon* in some parsimonious trees, the addition of outgroups did not alter the inferred structure of *Bracteon* itself (except, of course, to indicate its root).

As a complement to the relatively bold hypothesis presented in Figure 292, a more cautious view is illustrated in Figure 293. The latter is a summary of all of the trees summarized in Figure 292, plus all of the rest of the most-parsimonious trees inferred under all three weighting schemes, as well as the trees found from the recoded matrix. Note that some structure is present in the conservative tree of Figure 293 outside of *Bracteon*. *B. interventor* is the sister group of the rest of the examined *Bembidion;* the subgenera *Hirmoplataphus* (*B. concolor* and *B. salebratum*) and *Pseudoperyphus* are suggested to be monophyletic. Some aspects of the structure of *Pseudoperyphus* also are constant across trees. The *Odontium* subgeneric group is monophyletic in almost all of the trees. There is one exception. Forty of the trees, among the most parsimonious if error-prone and polymorphic characters are devalued, and if *Bracteon* is forced to be monophyletic, show *Pseudoperyphus* interposed between a clade containing *B.* sp. nr. *aenulum*, *B. chloropus*, *B. fusiforme*, and *B. aeneipes* and the rest of the *Odontium* subgeneric group. *Odontium* is not monophyletic in the most-parsimonious trees. However, the shortest trees in which *Odontium* is a clade are only two steps longer than the most parsimonious (length = 655, based on 115 searches by PAUP), and thus the evidence against the monophyly of *Odontium* is not strong.

Summary. Four major hypotheses should be considered plausible, and examined more in future studies: that *Bracteon* is monophyletic, with relationships as shown in Figure 292, or that *B. balli* and *B. foveum* are outside of the rest of *Bracteon* (Fig. 284), or that *B. argenteolum*, *B. alaskense*, and *B. semenovi* are actually more closely related to the *B. aenulum*-*B. fusiforme* complex (Figs. 285, 286, 289, 290), or that *B. bifossulatum* belongs within *Bracteon* (Fig. 291). These hypotheses are most-parsimonious, or nearly so, for all weighting schemes used, and for the unrecoded and recoded matrices. All four hypotheses should be considered if one uses the phylogenetic conclusions presented here as the foundation for some ecological, behavioral, or physiological studies. However, if one wants a bolder phylogenetic hypothesis to test, I recommend that of Figure 292.

Fossil Material

The oldest *Bracteon* fossils are fragments from the Beaufort Formation of Banks and Meighen islands. They are apparently Middle to Late Miocene, approximately 7–13 million years before the present (Matthews, 1976, 1977, 1979). I have examined 12 of these fragments, as well as 2 Early Holocene/Late Pleistocene fragments from Vermont (all JVMa!), identifiable with some certainty as *Bracteon*. Character states of these pieces are shown in Table 6.

Unfortunately, exact placement of any of these specimens on an inferred phylogeny is impossible, due to the lack of visible character states. Nonetheless, some assignments can be made.

For example, specimen B7 from Banks Island (JVM 3-73) is clearly a fragment of a *Bracteon* elytron (as a silver spot is present), but third interval elytral mirrors are lacking. The specimen thus belongs to the *B. balli-B. foveum* line, the stem-group of the rest of *Bracteon* (from a lineage predating the evolution of mirrors), or from the stem-group of *Bracteon*.

Some of the other elytral fragments possess mirrors, and thus belong to the "mirrored clade" of *Bracteon*. Placement beyond this is difficult, and of questionable validity. The specimens are phenetically most similar in visible features to *B. levettei*, but many of these similarities are symplesiomorphies. Cladistically they could fall nearly anywhere within the mirrored *Bracteon*.

The most notable features of the three pronota are the lack of a long basilateral carina and the presence of midlateral setae. There are a number of *Bracteon* lineages to which they might belong. As with the elytral fragments, the known pronota unfortunately contribute scant information about *Bracteon* evolution.

A few Pleistocene fragments have also been discovered. The only specimen from North America with which I am familiar is an elytron, probably of *B. levettei*, from southern Ontario; this specimen is from well within the range of present-day *B. levettei*. Coope (1969, 1979b) reports *B. velox* from Late Würm Glacial (Zone I) and Early Windermere Interstadial (13,200–12,000 years b. p.) deposits in Britain. This species is not extant in Britain, although it occurs across the English Channel in France (Fig. 266). From Glacial sediments just predating the Windermere Interstadial of the Isle of Man (about 19,000 years b. p.), fragments of *B. lapponicum* have been discovered (Coope, 1977, 1979a). *B. lapponicum* is now absent from the British Isles, occurring in northern Scandinavia (Fig. 267); its presence 19,000 years ago in Britain reflects the cooler climate at the time (Coope, 1977, 1979a). *B. litorale* is known from Early Windermere Interstadial (13,200–12,000 years b. p.) deposits in the British Isles (Coope, 1979b); this is within the modern geographic distribution of the species. The Pleistocene material, therefore, contains possibly Recent species in not-unexpected localities.

GENERAL PATTERNS OF EVOLUTION IN *BRACTEON*

A few general patterns in the data are worthy of note and discussion. The patterns pose more questions than they answer, and are noted here more for incentive they may provide for future research, than for the conclusions they yield.

Evolution of Mirrors

A most noticeable feature of many adult *Bracteon* is the presence of elytral mirrors. Why mirrors evolved is a puzzle. The mosaic pattern created by the mirrors is similar to that produced by pigment in other *Bembidion* (for example, many members of *Notaphus*). Microsculpturally mosaic elytra have evolved independently a number of times in caraboids (a few examples are *Systolosoma*, *Elaphrus*, *Opisthius*, *Scopodes*, *Tillius*, and *Asaphidion*). Perhaps the mosaic pattern confuses potential predators; at least in humans, "these patches tend to catch the eye of the observer and to draw his attention away from the shape which bears them" (Cott, 1940:48). Or perhaps mirrors are for thermoregulatory purposes; or perhaps there is some other function (see Lindroth, 1974b); or perhaps there is no function at all.

In his study of *Elaphrus*, Goulet (1983) notes a striking correlation between overall shininess of the beetles and substrate moisture, with shinier beetles occurring on wetter soils; as well, more extensively mirrored *Elaphrus* tend to occur on wetter substrates. Within *Bracteon*, the limited knowledge I have of habitats reveals no correlation between microsculpture and substrate. For example, unmirrored, dull beetles such as *B. foveum* and *B. balli* coexist in the same microhabitat with extensively mirrored, relatively shiny species such as *B. levettei*. Goulet (1983) explains the patterns he notes as resulting from evolutionary development of crypsis in response to predation; clearly, no such explanation is readily available for *Bracteon*. I cannot think of adaptive reasons for the divergence of microsculpture.

Evolution of Larvae

The *Bracteon* larvae with the most primitive features are found in the clade with 20 autosomes (*B. hesperium* + *B. lorquinii* + *B. inaequale*-subgroup). Almost all of the evolution of larvae detected within *Bracteon* has taken place within the less-mirrored members of the mirrored clade (Fig. 295). Genitalic characters show changes in similar parts of the tree as do adult external characters (compare Fig. 296 with 294), with the exception of *B. punctatostriatum*, which shows many derived features of adult structure, but may have no derived features detected in genitalia. Again, it is difficult to select any specific hypothesis explaining these patterns without more basic data about the natural history of *Bracteon* species.

One notable correlate is the presence in *B. carinula* of both the longest second stylomeres (Fig. 154) and the largest egg bursters (Figs. 228 and 234) of any *Odontium* subgeneric group members. Perhaps the long S2s are suited for laying eggs in an unusual microhabitat, a place that requires tougher chorion, which in turn requires larger egg bursters. A comparative study of the habits of *B. carinula* and related species, as well as discovery of larvae of the long-stylomered *B. robusticolle*, could provide rewarding tests of this hypothesis.

HISTORICAL MOVEMENTS OF *BRACTEON* LINEAGES

As with phylogeny reconstruction, historical biogeography can be approached from either a statistical or parsimony perspective. One could produce maximum likelihood estimates of the biogeographic history of a group, if one built a general model of the biogeographic behavior of lineages of the animals, and used it with presumed phylogenetic and geologic history. This would involve background assumptions about the dispersal abilities, natural history, etc., of the organisms. Such an analysis could be conducted with or without the aid of a computer. To my knowledge, statistical biogeographic methods for single clades (as opposed to whole biotas [Rosen, 1978, Simberloff, *et al.*, 1981]) remain wholly undeveloped. The reasons for this probably include the mathematical difficulties involved, as well as the lack of sufficient knowledge about most groups necessary to apply such techniques. Such methods would undoubtedly be opposed by cladists seeking to produce patterns using a minimum of process hypotheses; they would instead use cladistic biogeographic techniques. These techniques choose hypotheses that invoke vicariance as much as possible, and dispersal as little as possible, in explaining geographic distributions. This is advocated by its practictioners as a parsimony method, because the number of hypothesized dispersal events is minimized. The explanations I present for geographic distributions of *Bracteon* species invoke a mixture of vicariance and dispersal, and were arrived at with traditional (non-numerical) methods.

Dispersal has undoubtedly played a prominent role in the history of *Bracteon*, and has resulted in the sympatry (Table 1) and the wide ranges of most of the taxa. As can be seen from the distribution maps (Figs. 261–274), many *Bracteon* are widespread with coincident ranges. For example, within the Nearctic region, *B. carinula*, *B. punctatostriatum*, *B. levettei*, and *B. inaequale* are all transamerican, occurring from the Yukon Territory south into the contiguous United States. This overlap of species ranges has led to a clouding of vicariant patterns. One should thus expect only a few fragments of the geographic history of these widespread, lowland forms to be detectable. If one takes a cautious approach, and uses the phylogeny of Figure 293 as a foundation for biogeographic studies (Fig. 297), the lack of resolution in that phylogeny will lead to uncertainties in the inferences made. Ecological requirements of *Bracteon* lineages, when more thoroughly known, might provide additional clues.

Eight of the 18 taxa have restricted distributions (*B. balli*, *B. semenovi*, *B. stenoderum*, *B. hesperium*, *B. lorquinii*, *B. zephyrum*, *B. levettei levettei*, and *B. conicolle*). Three of these, *B. balli*, *B. semenovi*, and *B. conicolle*, are all near the edge of the range of what may be their widespread sister-groups.

B. balli occupies a small area in Alberta and Saskatchewan (Fig. 261), just within the southernmost limit of the range of *B. foveum* (Fig. 262). A relatively recent vicariance event may have split the common ancestor of these two species, with subsequent dispersal of one or both forms until *B. foveum* attained sympatry with *B. balli*. *B. foveum* populations presumably spent Quaternary glaciations in Nearctic Beringia or in the Palearctic, although they may have been south of the ice sheets in North America. However, it does seem most reasonable that *B. balli* occurred south of the ice sheets, with invasion northward upon glacial retreat. Indeed, the ice sheets may have been the barrier that allowed differentiation of the ancestral *B. foveum*-*B. balli* stock into the two extant species.

B. semenovi is only known from the holotype, found in a region which has been scantily collected (Fig. 263). The full range of the species is unknown, and thus biogeographic hypotheses about the species must be considered tentative. Nonetheless, it does seem reasonable to presume an isolation of a southern portion of the proto-*B. argenteolum*-*B. semenovi* stock resulting in divergence and separation of *B. argenteolum* and *B. semenovi*. An east-west vicariance probably resulted in the production of the *B. alaskense* lineage. The lack of cladistic resolution of the *B. argenteolum*-subgroup may be indicative of an actual trichotomy, that is, a near-simultaneous formation of the *B. semenovi* and *B. alaskense* lineages.

The 2n = 20+XY clade originated in the Nearctic, with most of its history in that region. Only relatively recently has one of its stocks (*B. litorale*-*B. conicolle*) invaded the Old World, with subsequent differentiation of eastern *B. conicolle* from western *B. litorale* (Fig. 274).

The three primitive species of the 2n = 20+XY clade (*B. hesperium*, *B. lorquinii*, and *B. zephyrum*) are isolated in western North America from British Columbia south to California (Figs. 269–271), whereas the derived members of the *B. inaequale*-subgroup are more widespread in the eastern and northern Nearctic, and in the Palearctic (Fig. 297). The Pacific coastal forms may have arisen as buddings from a more widespread Nearctic stock, with one of the buddings (that leading to *B. zephyrum*) invading the seashore. However, a full explanation of this pattern awaits a resolution of their relationships.

The relatives of *Bracteon*, *Odontium* and *Ochthedromus*, are predominantly southern groups. Within both the New and Old World, species of the latter two groups increase in numbers southward, at the expense of *Bracteon* diversity. *Bracteon* are thus more cool-adapted than their relatives, and probably have been throughout their history; whether the entire *Odontium* subgeneric group assemblage originated as cool or warm adapted animals, is not known.

Exactly when the ancestor of *Bracteon* arose is a mystery. It clearly was before the Late Miocene; in fact, the mirrored clade was already in existence by then. I hesitate to speculate age of origin, because of the lack of an adequate fossil record, and the lack of well-supported, detailed biogeographic hypotheses.

CONCLUSIONS

Darlington (1971a), in his review of the history of *Bembidion* systematics, notes the shift in emphasis from the time of Casey to that of Lindroth. From a view of systematics as a sorting of dead specimens, to Lindroth's studies of populations of living, evolving creatures, the change has encompassed an increasing knowledge of the organisms and their histories. Erwin and Kavanaugh's (1981, in prep.) studies have continued the progress, adding female genitalic characters to our data base, as well as introducing cladistic techniques. I have incorporated more adult structural characters, as well as larval and chromosomal features, along with modified cladistic techniques.

But, as always, much remains to be done; a few avenues of research that appear to me to be potentially valuable are worthy of note. I have only skimmed the surface of geographic variability of *Bracteon* species. *B. inaequale, B. lapponicum*, the *B. argenteolum*-subgroup, and *B. litorale*-*B. conicolle* all require further analysis. A study of external structural variation is warranted, as is that of any other character that might help sort out patterns of gene flow. Numerous morphological characters await study, including the microsculpture of the internal sac of male genitalia, as well as molecular data. A great aid to further phylogenetic analysis of *Bracteon* would be a more thorough study of interrelationships of outgroups. Examination of adults and larvae of *B. aenulum* and its East Asian relatives is crucial to the resolution of the issue of *Bracteon* monophyly. Some of the pathways of *Bracteon* evolution may then become clearer.

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Table 1. Sympatry in *Bracteon*. Species abbreviations: bl = *B. balli*, fo = *B. foveum*, ar = *B. argenteolum*, al = *B. alaskense*, sm = *B. semenovi*, st = *B. stenoderum*, ca = *B. carinula*, vx = *B. velox*, lp = *B. lapponicum*, pn = *B. punctatostriatum*, hs = *B. hesperium*, lq = *B. lorquinii*, ze = *B. zephyrum*, lvl = *B. levettei levettei*, lvc = *B. levettei carrianum*, in = *B. inaequale*, lt = *B. litorale*, co = *B. conicolle*. Other abbreviations: S = species found sympatrically but not known to occur at exact same locality, M = species found microsympatrically, together on the same beach, · = specimens not known to occur sympatrically.

Species	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
B. balli	—																	
B. foveum	M	—																
B. argenteolum	·	S	—															
B. alaskense	·	S	·	—														
B. semenovi	·	·	·	·	—													
B. stenoderum	·	·	·	·	·	—												
B. carinula	M	M	·	·	·	·	—											
B. velox	·	M	M	·	·	·	·	—										
B. lapponicum	M	M	M	M	·	·	M	·	—									
B. punctatostriatum	M	M	·	·	·	·	M	·	M	—								
B. hesperium	·	·	·	·	·	·	·	·	S	S	—							
B. lorquinii	·	·	·	·	·	·	·	·	S	S	M	—						
B. zephyrum	·	·	·	·	·	·	·	·	S	S	S	S	—					
B. levettei levettei	·	·	·	·	·	·	·	·	S	M	S	S	·	—				
B. levettei carrianum	M	M	·	M	·	·	M	·	M	M	·	·	·	·	—			
B. inaequale	M	M	·	S	·	·	M	·	M	M	M	M	S	M	M	—		
B. litorale	·	M	M	·	·	·	·	M	M	·	·	·	·	·	·	·	—	
B. conicolle	·	M	S	S	·	S	·	·	S	·	·	·	·	·	·	·	M	—

Table 2. Character states in *Bracteon*. Species abbreviations: bl = *B. balli*, fo = *B. foveum*, ar = *B. argenteolum*, al = *B. alaskense*, sm = *B. semenovi*, st = *B. stenoderum*, ca = *B. carinula*, vx = *B. velox*, lp = *B. lapponicum*, pn = *B. punctatostriatum*, hs = *B. hesperium*, lq = *B. lorquinii*, ze = *B. zephyrum*, lvl = *B. levettei levettei*, lvc = *B. levettei carrianum*, in = *B. inaequale*, lt = *B. litorale*, co = *B. conicolle*. Other symbols: "0, 1" = taxon dimorphic, with both states 0 and 1; "0–2" = taxon polymorphic, with states 0 through 2; "?" = character state unknown; "—" = character state not applicable. Number of specimens examined for each entry listed in Table 3.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
Adult external characters																		
1. Silver spots 0 = absent; 1 = present	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2. Mirrors on interval 3 0 = absent; 1 = very slightly shinier; 2 = slight mirrors; 3 = distinct mirrors	1	1	3	3	2	3	3	3	3	3	2, 3	3	3	3	3	3	3	3
3. Mirrors on intervals 4 or 5 0 = absent; 1 = very slightly shinier; 2 = slight mirrors; 3 = distinct mirrors	1	1	2, 3	2, 3	2	3	0–2	0–2	0–3	0–2	3	3	3	3	3	3	3	3
4. Mirrors on intervals 6 or 7 0 = absent; 1 = very slightly shinier; 2 = slight mirrors; 3 = distinct mirrors	0	0	0, 1	0	0	0, 2	0	1	0, 2	1	0, 2	1	2, 3	3	3	3	3	3
5. Interval 7 mirror isolated? 0 = no; 1 = yes	—	—	—	—	—	0	—	—	0	—	0	—	0	0	0	0, 1	0, 1	0, 1
6. Silver spot on interval 4? 0 = no, restricted to 3rd; 1 = yes	0	0	0	0, 1	0	0	0	0	0	0	0, 1	0, 1	0, 1	1	1	0, 1	0, 1	0, 1
7. Elytral sculpticell shape 0 = isodiametric; 1 = slightly transverse; 2 = transverse	0	0	0	0	0	0	0	0	0	0	0–2	0	0	0	0	0	0	0
8. Suborbital setae 0 = absent, Fig. 60; 1 = short and sparse; 2 = denser, Fig. 59	1, 2	1, 2	2	2	2	1, 2	2	2	2	0	1	0, 1	2	2	2	0–2	2	2
9. Midlateral pronotal setae 0 = absent; 1 = present	1	1	0	0	0	0	1	1	1	1	0	0	1	1	1	0, 1	0, 1	0
10. ed3 and ed5: position relative to 3rd stria 0 = "free," in interval; 1 = attached to stria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
11. ed3 and ed5: position relative to silver spot 0 = anterior end of spot; 1 = center of spot	0	0, 1	0	1	0	0	0, 1	0	0, 1	0	0	0	1	0, 1	0, 1	0, 1	0, 1	0
12. Setae between eo4 and eo5 (average number) (discrete coding for numerical analysis: 0 = <0.40; 1 = 0.40–0.80; 2 = 1.8–2.1; 3 = >3.0)	0.05	0.80	1.8	0.10	4	0	0.40	0	0.09	2.1	0	0.07	0	0	0	0.04	0	0.14
13. Number setae ed7 area (average number) (discrete coding for numerical analysis: 1 = 0.90–1.1; 2 = 1.9–2.1)	1	1.1	0.92	1	1	1.9	1	1	1.1	1	1	1	1	1	1	1	1	1
14. Male adhesive setae 0 = narrow, Fig. 86; 1 = wide, Figs. 84, 85	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
15. Protarsomere 4 ventroapical setae 0 = less flattened, more circular, Fig. 94; 1 = apically flattened, wide, Fig. 96	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	?
16. Protarsomere 4 setal separation 0 = narrow, Figs. 93–96; 1 = wide, Fig. 92	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17. Mandible shape 0 = curved, Fig. 25; 1 = straight, narrow, Fig. 28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18. Lacinia shape 0 = curved, Figs. 44–48; 1 = straight, narrow, Fig. 42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19. Lacinia width 0 = narrow, Figs. 46, 47; 1 = wide, Fig. 48	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
20. Mentum tooth shape 0 = triangular, trapezoid; 1 = subrectangular; 2 = rectangular, with deep lateral incisions	0	0	0	0	0	0	0	0	0	2	0	0	2	2	2	2	0	2
21. Mentum tooth emarginate? 0 = no; 1 = yes	0	0	0, 1	0, 1	1	0	0	0	0	0	0, 1	1	0, 1	0	0	0	1	0, 1
22. Mentum tooth bulbous? 0 = flat; 1 = slightly bulbous; 2 = distinctly bulbous	0	0	0	0	0	0	0	0	0	2	0	0	0	2	2	2	0	1
23. Mentum epilobes 0 = absent, Figs. 52, 55; 1 = indistinct; 2 = distinct, Figs. 49–51	2	2	2	2	2	2	2	2	2	0	2	2	2	0	0	0	2	2
24. Pronotal shape 0 = rounded sides; 1 = trapezoid, prominent anterior corners	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25. Pronotal carina 0 = absent; 1 = short, separated from base, Fig. 71; 2 = long, separated from base; 3 = long, attached to base, Fig. 70	0, 1	0, 1	0, 1	0	0	1	3	0, 1	1	0, 1	0, 1	0, 1	0, 1	0, 1	0, 1	0, 1	0	0, 1
26. Metasternum 0 = unbordered; 1 = bordered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27. Elytral basal impression 0 = absent; 1 = slight; 2 = definite	2	2	0	0	0	0	1, 2	0, 1	1	0, 1	1, 2	2	2	2	2	0–2	1, 2	1, 2
28. Angulate humeral margin 0 = absent; 1 = short, Figs. 69, 73; 2 = moderate, Figs. 68, 70; 3 = long, Figs. 71, 72	1, 2	1	2	1	2	3	2	3	3	3	1	1	1	1	1	1	1	1
29. Stria 4 shape 0 = straight; 1 = slightly sinuate; 2 = distinctly sinuate	0	0	0	0	0	0	0	0	0	0	0	0	0–2	0–2	2	2	1, 2	0, 1

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
30. Elytra around ed3 and ed5 0 = not foveolate; 1 = slightly foveolate; 2 = foveolate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31. Elytral punctures 0 = circular; 1 = slightly transverse; 2 = transversely stretched	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0, 1	0	0
32. Stria 8 depth 0 = as shallow as 7th anteriorly; 1 = slightly deeper than 7th anteriorly; 2 = distinctly deeper than 7th anteriorly	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0, 1	0	0
33. Interval 5 posteriorly 0 = flat; 1 = ridged	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34. Subapical elytral plica 0 = absent; 1 = internal only, not connected to epipleuron; 2 = connected to epipleuron	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
35. Male protarsomere 3 shape 0 = no lateral projection, Figs. 75–77; 1 = slight projection; 2 = prominent projection, Fig. 78	0	0	0	0, 1	2	0	0	0	0, 1	0	0	0	0	0	0	0	0	0
36. Protarsomere 4 projection 0 = absent, minute, Figs. 90–94; 1 = very short; 2 = short, Fig. 95; 3 = long, Fig. 96	3	3	0	0	1	3	3	3	2	0	2	2	2	2	2	2	2	2
Male genitalia																		
37. Flagellar sheath 0 = as Figs. 112, 113, 117–128; 1 = dark and hooked, Figs. 114–116	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
38. Flagellar sheath sculpture 0 = without long, thin scales; 1 = with long, thin scales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
39. CSC right lobe 0 = absent; 1 = present, ventral margin narrow; 2 = present, ventral margin moderate; 3 = present, ventral margin wide	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
40. CSC right lobe ridge 0 = no ridge; 1 = slightly; 2 = distinctly	0	0	0	0	0	2	0	2	2	0, 1	0, 1	2	0	0	0	0	0	0
41. VSP dorsal ridge 0 = not angled, Figs. 112–120; 1 = very slightly; 2 = slightly; 3 = sharply angled, Figs. 124–128	0	0	0	0	0	0	0	0	0	0	1	2	1	3	3	3	3	3
42. VSP dorsal ridge sculpture 0 = unscaled; 1 = slightly scaled; 2 = distinctly scaled	2	2	2	2	2	0	0	0	0	0	0	0	0	2	2	2	0	0
43. Dark spot on flagellar sheath 0 = absent; 1 = present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44. Ostial microtrichial patch size 0 = absent; 1 = small, Fig. 116; 2 = medium (not dorsal), Figs. 114, 115; 3 = large; 4 = very large, dense, dorsal, Figs. 112, 113	4	4	2	2	2	1	2	4	4	4	4	4	4	4	4	4	4	4
45. Ostial scales 0 = comb-like scales larger; 1 = combs sparse, small	0	0	—	—	—	—	—	—	0	—	0	—	0	—	—	—	—	—
46. Ostial microtrichial patch 0 = comb-like scales absent; 1 = combs few; 2 = combs extensive; 3 = combs extensive, sparse, small	2	2	0	0	0	0	0	0	1	0	0, 1	0	2	0	0	0	0	0
47. Ostial sclerotized strip 0 = absent, Figs. 123, 124; 1 = present, Figs. 126–128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1

Table 2. Continued.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
48. Ostial strip sculpture 0 = not beaded; 1 = beaded	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0
49. Pillow with scales 0 = absent; 1 = present, Fig. 119	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
50. Internal sac, leftmost central membrane 0 = small scales; 1 = large scales, Fig. 108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51. Ventral bulge 0 = absent; 1 = slight; 2 = distinct, Fig. 126	0	0	0, 1	1	0	0	0	0	0	0	0, 1	0, 1	0, 1	0	0	2	0	0
52. Aedeagal apex 0 = straighter; 1 = abruptly ventrally bent	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Female genitalia																		
53. Vaginal sclerotized plate 0 = absent; 1 = present	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
54. Spermatheca apically indented? 0 = no; 1 = yes	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
55. Stylomere 1 setal length 0 = absent; 1 = short, Fig. 154; 2 = medium; 3 = long, Fig. 152	2	2	2	2	?	3	1	2	2	2	2	2	2	2	2	2	2	2
56. Stylomere 2 length (μm, average) **B. zephyrum* varies from 190 to 325 micrometers (discrete coding for numerical analysis: 0 = <210; 1 = 210–300; 2 = 300–400; 3 = >400)	168	171	361	310	?	154	410	194	188	198	219	174	*	186	169	158	190	167
57. Number dorsolateral sensilla	2	2	2–4	3, 4	?	2	4–6	1, 2	1, 2	2, 3	0	1, 2	1–3	2, 3	2, 3	1, 2	2	2
58. Sternum X setae 0 = very short, nubbin-like; 1 = longer	1	1	1	1	?	1	0	1	1	1	1	1	1	1	1	1	1	1

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
Chromosomes																		
59. Pairs of autosomes, count for *B. litorale* from Nettman (1986) (Discrete coding for numerical analysis: 0 = 10; 1 = 11; 2 = 12; 6 = 16; 7 = 17)	11	11	?	11	?	?	11	?	11	11	10	10	10	10	10	10	17	?
60. Y chromosome size 0 = absent; 1 = small, <⅔ autosome size; 2 = medium, ⅔–1 autosome size; 3 = large, about autosome size	3	3	?	1	?	?	1	?	3	3	2	2	3	?	2, 3	2	?	?
First instar larva																		
61. Frontale with three spots 0 = not distinctly; 1 = slightly; 2 = distinctly	2	2	0	0	?	?	0	?	0	2	2	2	0–2	2	2	2	?	?
62. Head (other than spots) 0 = light; 1 = centrally dark; 2 = dark	2	2	1	1	?	?	1	?	2	0	0	0	0	0	0	0	?	?
63. Frontale behind FR_3 0 = microsculpture absent, Figs. 227, 228; 1 = laterally only, microsculpture slight; 2 = laterally only, Figs. 229, 231; 3 = centrally, Fig. 230	2	2	?	0	?	?	0	?	2	3	2	2	2	2	2	2	?	?
64. Frontale: anteriorly behind FR_3 0 = microsculpture absent; 1 = single-toothed denticles; 2 = rare multitoothed combs; 3 = some multitoothed combs	2	3	?	0	?	?	0	?	1	1	1	1	1	1	1	1	?	?
65. Parietal eggbursters 0 = small denticles, Figs. 226, 230, 231; 1 = small teeth, Figs. 227, 229; 2 = large teeth, spaced; 3 = large teeth, clustered, Fig. 228	0	0	?	1	?	?	3	?	1	0	0	0	0	0	0	0	?	?

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
66. Pronotal microtubercles 0 = absent; 1 = present only laterally; 2 = laterally, faint centrally; 3 = absent between PR_{14}; 4 = absent only before PR_{14}; 5 = prominent throughout	1	1	?	0	?	?	0	?	2	4	0	0	0	0	0	0	?	?
67. FR_1 width 0 = <½ FR_2 width; 1 = >½ FR_2 width	0	0	?	0	?	?	1	?	1	0	0	0	0	0	0	0	?	?
68. FR_3 width 0 = <½ FR_2 width; 1 = >½ FR_2 width	0	0	?	0	?	?	1	?	1	1	0	0	0	0	0	0	?	?
69. PR_4 length 0 = very short; 1 = short, Fig. 241; 2 = long, Fig. 240	2	2	?	2	?	?	2	?	2	1	2	2	2	2	2	2	?	?
70. PR_{10} length 0 = absent; 1 = short, Fig. 243; 2 = medium, Fig. 244; 3 = long, Fig. 242	3	3	?	3	?	?	1	?	3	0	3	3	3	3	3	3	?	?
71. gPR and gME lateral setae 0 = absent; 1 = present, Figs. 237, 241	0	0	?	0	?	?	0	?	0	1	0	0	0	0	0	0	?	?
72. PR_{13} length 0 = short; 1 = long	1	1	1	1	?	?	0	?	1	1	1	1	1	1	1	1	?	?
73. ME_2 length VS = very short, Fig. 246; S = short; M = medium, Fig. 247; L = long, Fig. 248	3	3	?	3	?	?	0	?	0	1	3	3	3	3	3	3	?	?
74. ME_{14} length 0 = very short; 1 = short; 2 = medium; 3 = long	3	3	3	3	?	?	0	?	3	3	3	3	3	3	3	3	?	?
75. TE_6 length 0 = very short, Fig. 253; 1 = short, Fig. 254; 2 = long, Fig. 252	2	2	?	2	?	?	0	?	0	1	2	2	2	2	2	2	?	?

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
76. TE_{11} length 0 = very short, Fig. 250; 1 = short; 2 = long, Fig. 248	2	2	2	2	?	?	0	?	2	2	2	2	2	2	2	2	?	?
77. TE_{11} shape 0 = narrow, parallel-sided, Fig. 249; 1 = basally wide, tapered, Fig. 248	1	0	?	1	?	?	?	?	1	1	1	1	1	1	1	1	?	?
78. TE_{α} 0 = absent; 1 = present, Fig. 251	0	0	?	0	?	?	0	?	0	1	0	0	0	0	0	0	?	?
79. EP_1 length 0 = short, Fig. 251; 1 = long, Fig. 248	1	1	?	1	?	?	1	?	1	0	1	1	1	1	1	1	?	?
80. Segment VIII EP_1 width 0 = <⅓ EP_2 width; 1 = >½ EP_2 width	0	0	?	0	?	?	1	?	1	?	0	0	0	0	0	0	?	?
81. Seta ST_2 on segment IX 0 = absent; 1 = present, Fig. 256	0	0, 1	?	0	?	?	1	?	1	0	0	0	0	0	0	0	?	?
82. Mandible mesal margin 0 = shelf absent, Fig. 200; 1 = minute shelf; 2 = narrow shelf, Fig. 199; 3 = wide shelf, Fig. 198	2	2	?	0	?	?	3	?	3	1	0	0	0	0	0	0	?	?
Second instar larva																		
83. Extra setae near FR_3 0 = absent; 1 = present	0	?	?	1	?	?	1	?	0	0	0	0	0	0	0	0	?	?
84. L2 stipites 0 = 3 outer setae; 1 = 4 outer setae	0	?	?	0	?	?	0	?	0	0	0	0	0	0	0	0	?	?
85. Long urogomphus setae, see Figs. 258–260 0 = 7 = setae; 2 = 9 setae; 3 = 10 setae	0	?	?	0	?	?	3	?	2	0	0	0	0	0	0	0	?	?

TABLE 3. NUMBERS OF SPECIMENS OF *BRACTEON* STUDIED. LARGER NUMBERS (E.G., "100") APPROXIMATE. DOTS ("·") INDICATE NO SPECIMENS EXAMINED FOR THIS CHARACTER. SPECIES ABBREVIATIONS: BL = *B. BALLI*, FO = *B. FOVEUM*, AR = *B. ARGENTEOLUM*, AL = *B. ALASKENSE*, SM = *B. SEMENOVI*, ST = *B. STENODERUM*, CA = *B. CARINULA*, VX = *B. VELOX*, LP = *B. LAPPONICUM*, PN = *B. PUNCTATOSTRIATUM*, HS = *B. HESPERIUM*, LQ = *B. LORQUINII*, ZE = *B. ZEPHYRUM*, LVL = *B. LEVETTEI LEVETTEI*, LVC = *B. LEVETTEI CARRIANUM*, IN = *B. INAEQUALE*, LT = *B. LITORALE*, CO = *B. CONICOLLE*.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
1. Silver spots	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
2. Mirrors on interval 3	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
3. Mirrors on intervals 4 or 5	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
4. Mirrors on intervals 6 or 7	20	20	20	20	1	20	50	20	20	20	20	20	100	50	100	100	50	20
5. Interval 7 mirror isolated?	·	·	·	·	1	20	·	·	20	·	20	·	100	50	100	100	50	20
6. Silver spot on interval 4?	10	10	10	10	1	10	10	10	10	10	10	10	10	10	10	10	10	10
7. Elytral sculpticell shape	6	6	6	6	1	15	6	6	6	6	6	6	6	6	6	6	6	6
8. Suborbital setae	6	7	7	7	1	7	7	7	7	7	7	7	7	7	7	7	7	7
9. Midlateral pronotal setae	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
10. ed3 and ed5: position relative to 3rd stria	10	10	10	10	1	10	10	10	10	10	10	10	10	10	10	10	10	10
11. ed3 and ed5: position relative to silver spot	20	10	20	10	1	10	10	10	10	15	10	10	10	10	10	10	10	10
12. Setae between eo4 and eo5	20	20	20	20	1	12	20	11	11	14	10	14	15	15	15	30	13	7
13. Number setae ed7 area	12	12	12	12	1	12	12	12	12	12	12	12	12	12	12	20	12	12
14. Male adhesive setae	5	5	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
15. Protarsomere 4 ventroapical setae	5	5	5	7	1	6	6	4	5	5	5	6	4	3	2	2	3	2
16. Protarsomere 4 setal separation	6	6	10	7	1	6	6	4	7	8	7	6	6	7	7	11	7	2
17. Mandible shape	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
18. Lacinia shape	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
19. Lacinia width	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
20. Mentum tooth shape	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
21. Mentum tooth emarginate?	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
22. Mentum tooth bulbous?	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
23. Mentum epilobes	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
24. Pronotal shape	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
25. Pronotal carina	16	20	20	20	1	20	70	30	40	20	20	20	20	20	20	20	20	20
26. Metasternum	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
27. Elytral basal impression	12	20	12	12	1	12	25	12	12	12	12	12	12	12	12	12	12	12
28. Angulate humeral margin	20	20	8	8	1	8	8	8	8	8	8	8	8	8	8	8	8	8
29. Stria 4 shape	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
30. Elytra around ed3 and ed5	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
31. Elytral punctures	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	6	6	6

TABLE 3. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
32. Stria 8 depth	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	6	6	6
33. Interval 5 posteriorly	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
34. Subapical elytral plica	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
35. Male protarsomere 3 shape	5	4	10	7	1	5	4	5	7	5	6	5	6	3	3	6	4	3
36. Protarsomere 4 projection	7	7	6	4	1	7	5	4	6	6	6	6	5	6	8	11	6	4
37. Flagellar sheath	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3
38. Flagellar sheath sculpture	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3
39. CSC right lobe	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
40. CSC right lobe ridge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
41. VSP dorsal ridge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
42. VSP dorsal ridge sculpture	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
43. Dark spot on flagellar sheath	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
44. Ostial microtrichial patch size	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
45. Ostial scales	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
46. Ostial microtrichial patch	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
47. Ostial sclerotized strip	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
48. Ostial strip sculpture	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
49. Pillow with scales	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
50. Internal sac leftmost central membrane	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
51. Ventral bulge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
52. Aedeagal apex	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
53. Vaginal sclerotized plate	5	6	7	5	·	3	5	5	5	5	5	5	5	5	5	9	3	2
54. Spermatheca apically indented?	3	3	3	3	·	3	3	3	3	3	3	3	3	3	3	3	3	3
55. Stylomere 1 setal length	5	6	7	5	·	3	5	5	5	5	5	5	5	5	5	9	3	2
56. Stylomere 2 length	3	3	4	4	·	3	3	3	3	3	3	3	43	3	5	6	3	2
57. Number dorsolateral sensilla	5	6	7	5	·	3	5	5	5	5	5	5	5	5	5	9	3	2
58. Sternum X setae	5	6	7	5	·	3	5	5	5	5	5	5	5	5	5	9	3	2
59. Pairs of autosomes	10	29	·	11	·	·	17	·	30	10	9	7	10	5	38	24	?	·
60. Y chromosome size	4	8	·	5	·	·	7	·	9	4	3	2	3	2	11	8	·	·
61. Frontale with three spots	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
62. Head (other than spots)	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
63. Frontale behind FR_3	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
64. Frontale: anteriorly behind FR_3	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
65. Parietal eggbursters	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·

TABLE 3. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
66. Pronotal microtubercles	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
67. FR_1 width	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
68. FR_3 width	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
69. PR_4 length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
70. PR_{10} length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
71. gPR and gME lateral setae	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
72. PR_{13} length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
73. ME_2 length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
74. ME_{14} length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
75. TE_6 length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
76. TE_{11} length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
77. TE_{11} shape	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
78. TE_α	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
79. EP_1 length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
80. Segment VIII EP_1 width	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
81. Seta ST_2 on segment IX	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
82. Mandible mesal margin	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
83. Extra setae near FR_3	2	·	·	3	·	·	2	·	1	1	2	1	1	1	2	2	·	·
84. L2 stipites	2	·	·	3	·	·	2	·	1	1	2	1	1	1	2	2	·	·
85. Long urogomphus setae	2	·	·	3	·	·	2	·	1	1	2	1	1	1	2	2	·	·

TABLE 4. CHARACTER STATES IN *ASAPHIDION ALASKANUM*, *BEMBIDION* DISTANTLY RELATED TO *BRACTEON*, AND *PSEUDOPERYPHUS*. SPECIES ABBREVIATIONS: ASA = *ASAPHIDION ALASKANUM* WICKHAM, QUA = *B. QUADRIMACULATUM* (LINNÉ) (FROM ALBERTA), TIM = *B. TIMIDUM* LECONTE, GRA = *B. GRAPHICUM* CASEY, UMB = *B. UMBRATUM* LECONTE, SCO = *B. SCOPULINUM* KIRBY, OBS = *B. OBSCURELLUM* MOTSCHULSKY, PET = *B. PETROSUM* GEBLER, CNC = *B. CONCOLOR* KIRBY, SAL = *B. SALEBRATUM* LECONTE, PLN = *B. PLANATUM* LECONTE, KUP = *B. "KUPRIANOVI-#1"* (THIS IS THE LARGER AND DARKER OF THE TWO SPECIES PRESENTLY INCLUDED WITHIN *B. KUPRIANOVI*), OBT = *B. OBTUSUM* SERVILLE, INV = *B. INTERVENTOR* LINDROTH, RUF = *B. RUFOTINCTUM* HAYWARD, INT = *B. INTEGRUM* CASEY, HON = *B. HONESTUM* SAY, ANT = *B. ANTIQUUM* DEJEAN, S17 = *B.* "SP. 17", CHA = *B. CHALCEUM* DEJEAN. OTHER SYMBOLS, INCLUDING THOSE FOR CHARACTER STATES, AS IN TABLE 2.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
Adult external characters																				
Number of specimens	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6	6	6	6	6	6
1. Silver spots	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. Mirrors on interval 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3. Mirrors on intervals 4 or 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4. Mirrors on intervals 6 or 7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5. Interval 7 mirror isolated?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6. Silver spot on interval 4?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7. Elytral sculpticell shape	2	—	0	2	0	2	0–2	2	2	2	0	2	2	2	0	2	0	0–2	2	2
8. Suborbital setae	2	1	0, 1	0, 1	0	0	0	0	1	0	1, 2	2	0	0, 1	1	0	2	2	1	1, 2
9. Midlateral pronotal setae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
10. ed3 and ed5: position relative to 3rd stria	—	0, 1	0	0	0	1	1	1	1	1	1	1	1	0, 1	1	1	1	1	1	1
11. ed3 and ed5: position relative to silver spot	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12. Setae between eo4 and eo5	0	0	0	0	0	0	0	0	0.13	0	0.25	0	0	0.14	0.14	0.14	0	0.15	0.17	0.08
13. Number setae ed7 area	1.1	1	1	1	1	1	1	1.1	1	1	1	1	1	1	1	1	1	1	1	1
14. Male adhesive setae	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
15. Protarsomere 4 ventroapical setae	0	0	0	1	?	1	?	1	1	?	1	1	?	0	1	1	1	1	1	1
16. Protarsomere 4 setal separation	1	1	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0
17. Mandible shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18. Lacinia shape	0	?	?	0	?	?	?	0	?	?	0	0	?	0	0	0	0	0	0	0
19. Lacinia width	0	?	?	?	?	?	0	0	?	?	0	0	0	1	0	0	0	0	0	0
20. Mentum tooth shape	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21. Mentum tooth emarginate?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
22. Mentum tooth bulbous?	0	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
23. Mentum epilobes	2	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2

TABLE 4. CONTINUED.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
24. Pronotal shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25. Pronotal carina	0	3	3	2	2	0, 1	2	2	2	0, 1	2	2	1, 2	1, 2	0	0	0	0	0	0
26. Metasternum	0	1	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0
27. Elytral basal impression	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28. Angulate humeral margin	0	0	0	0	0	0	0	0	0	1	0	1	2, 3	3	0	0	0	0	0	0
29. Stria 4 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30. Elytra around ed3 and ed5	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
31. Elytral punctures	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32. Stria 8 depth	?	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
33. Interval 5 posteriorly	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0
34. Subapical elytral plica	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
35. Male protarsomere 3 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36. Protarsomere 4 projection	0	0	2	2	2	?	?	3	?	?	2	?	?	0	?	2	2	2	?	2
Male genitalia																				
Number of specimens	2	2	2	1	1	2	2	1	2	2	2	2	2	1	3	2	3	4	4	4
37. Flagellar sheath	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
38. Flagellar sheath sculpture	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	1	1
39. CSC right lobe	?	1	1	0	0	1	1	1	1	1	1	0	1	0	3	3	3	3	3	3
40. CSC right lobe ridge	?	0	0	?	?	0	0	0	0	0	0	?	0	?	0	0	0	0	0	0
41. VSP dorsal ridge	?	?	?	?	?	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0
42. VSP dorsal ridge sculpture	?	?	?	?	?	?	0	?	2	2	2	2	?	?	0	0	0	0	1	0
43. Dark spot on flagellar sheath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44. Ostial microtrichial patch size	0	0	0	0	0	4	3	2	2	3	4	4	1	2	3	4	4	4	3	4
45. Ostial scales	—	—	—	—	—	0	—	0	—	—	—	0	—	0	0	0	0	0	—	—
46. Ostial microtrichial patch	—	—	—	—	—	2	0	2	0	0	0	2	0	2	1	2	2	1, 2	0	0
47. Ostial sclerotized strip	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
48. Ostial strip sculpture	—	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—
49. Pillow with scales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 4. CONTINUED.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
50. Internal sac leftmost central membrane	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
51. Ventral bulge	0	0	0	0	0	0	0	0	0	0	0	0	0, 1	1	0	0	2	1	1	1
52. Aedeagal apex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Female genitalia																				
Number of specimens	2	2	2	1	2	2	1	3	2	2	2	2	1	2	1	2	1	2	1	3
53. Vaginal sclerotized plate	1	1	0	1	1	0	0	0, 1	1	1	1	1	1	1	0	0	0	0	0	0
54. Spermatheca apically indented?	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
55. Stylomere 1 setal length	0	2	0	2	2	2	2	0, 2	3	2	0	2	0	0	3	3	3	3	3	3
56. Stylomere 2 length	170	130	95	140	125	125	160	150	140	125	250	170	110	165	170	190	170	220	190	160
57. Number dorsolateral sensilla	2, 3	2, 3	2	2	2	1–3	1, 2	1, 2	2, 3	2	0	2, 3	2	2	2, 3	2, 3	1, 2	2, 3	3, 4	2
58. Sternum X setae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Chromosomes																				
Number of specimens	10	4	3	5	4	3	2	7	2	2	7	2	4	7	8	4	3	12	8	11
59. Pairs of autosomes	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	16	12
60. Y chromosome size	1	?	?	1	1	?	?	0	2, 3	2, 3	1	1	1	?	?	2	2	2	1	2
First instar larva																				
Number of specimens	1	2	1	3	2	1	1	3	3	5	1	1	2	5		1		1		4
61. Frontale with three spots	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0
62. Head (other than spots)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0
63. Frontale behind FR_3	2	1	2	2	2	1	0	1	2	2	1	1	1	2	?	2	?	0	?	2
64. Frontale: anteriorly behind FR_3	1	?	3	3	3	1	?	1	1	2	1	1	1	1	?	3	?	0	?	3
65. Parietal eggbursters	1	0	0	0	0	0	0	0	0	0	1	0	0	1	?	0	?	0	?	0
66. Pronotal microtubercles	5	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0
67. FR_1 width	1	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	?	0	?	0
68. FR_3 width	1	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	?	0	?	0
69. PR_4 length	0	2	2	2	2	2	2	2	2	2	2	2	2	2	?	2	?	2	?	2
70. PR_{10} length	0	3	3	3	3	3	3	3	3	3	3	3	3	3	?	2	?	2	?	3
71. gPR and gME lateral setae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0

TABLE 4. CONTINUED.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
72. PR_{13} length	?	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	1	?	1
73. ME_2 length	3	3	3	3	3	3	3	3	3	3	3	3	3	3	?	3	?	2	?	3
74. ME_{14} length	?	3	3	3	3	3	3	3	3	3	3	3	3	3	?	3	?	3	?	3
75. TE_6 length	1	2	2	2	2	2	2	2	2	2	2	2	2	2	?	2	?	2	?	2
76. TE_{11} length	?	2	2	2	2	2	2	2	2	2	2	2	2	2	?	2	?	2	?	2
77. TE_{11} shape	?	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	1	?	1
78. TE_α	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0
79. EP_1 length	0	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	1	?	1
80. Segment VIII EP_1 width	?	1	1	0	0	1	1	1	1	1	1	1	1	0	?	0	?	?	?	1
81. Seta ST_2 on segment IX	0	0	0	0	0	0	0	0	1	1	0	0	0	0	?	0	?	?	?	0
82. Mandible mesal margin	0	1	1	2	2	3	2	0, 2	2	0, 2	2	3	2	0	?	2	?	3	?	3
Second instar larva																				
Number of specimens				1	1		1	1	1	1				1				1		
83. Extra setae near FR_3	?	?	?	0	0	?	0	0	0	0	?	?	?	0	?	?	?	0	?	?
84. L2 stipites	?	?	?	1	1	?	0	0	0	0	?	?	?	0	?	?	?	0	?	?
85. Long urogomphus setae	?	?	?	0	0	?	0	0	0	0	?	?	?	0	?	?	?	0	?	?

TABLE 5. CHARACTER STATES IN *OCHTHEDROMUS* AND *ODONTIUM*. SPECIES ABBREVIATIONS: AME: *B. AMERICANUM* DEJEAN, BIF: *B. BIFOSSULATUM BIFOSSULATUM* LECONTE, CHE: *B. BIFOSSULATUM CHEYENNENSE* CASEY, CHP: *B. CHLOROPUS* BATES, FUS: *B. FUSIFORME* NETOLITZKY, AEP: *B. AENEIPES* BATES, NRA: *B.* SP. NR. *AENULUM*, AEN: *B. AENULUM* HAYWARD, DUR: *B. DURANGOENSE* BATES, ARZ: *B. ARIZONAE* LINDROTH, CNF: *B. CONFUSUM* HAYWARD, SCU: *B. SCULPTURATUM* (MOTSCHULSKY), CRT: *B. CARINATUM* (LECONTE), COX: *B. COXENDIX* SAY, ROB: *B. ROBUSTICOLLE* HAYWARD, PRS: *B. PERSIMILE* MORAWITZ, STR: *B. STRIATUM* (FABRICIUS), FOR: *B. FORAMINOSUM* STURM, BOW: *B. BOWDITCHII* LECONTE. OTHER SYMBOLS, INCLUDING THOSE FOR CHARACTER STATES, AS IN TABLE 2.

Character	ame	bif	che	chp	fus	aep	nra	aen	dur	arz	cnf	scu	crt	cox	rob	prs	str	for	bow
Adult external characters																			
Number of specimens	4	6	6	3	3	6	2	6	4	6	6	5	2	6	4	6	6	6	6
1. Silver spots	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. Mirrors on interval 3	0	2	2	1	2	2	0	0	0	0	0	0	0	1	0	1	1	1	1
3. Mirrors on intervals 4 or 5	0	2	2	1	2	2	0	0	0	0	0	0	0	1	0	1	1	1	1
4. Mirrors on intervals 6 or 7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
5. Interval 7 mirror isolated?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6. Silver spot on interval 4?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7. Elytral sculpticell shape	0	1	1	0	0	0	2	0	0	2	2	1	1	0	0–2	0	0	0	0
8. Suborbital setae	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0, 1	0, 1	2	1	0
9. Midlateral pronotal setae	1	1	1	0	0	0	0	0	0	0	1	1	1	0, 1	1	1	1	1	1
10. ed3 and ed5: position relative to 3rd stria	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0, 1	1
11. ed3 and ed5: position relative to silver spot	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12. Setae between eo4 and eo5	0	0	0.14	0	0	0.10	0	0	0	0	0.08	0	0.33	0.08	0	0.10	0.08	0.08	0.29
13. Number setae ed7 area	1	1	1	1	1	1.1	1	1	1	1	1	1	1	0.94	1	1	1	1	1.1
14. Male adhesive setae	?	1	1	1	1	1	1	1	1	1	1	?	1	1	1	?	1	?	1
15. Protarsomere 4 ventroapical setae	?	1	1	?	?	?	1	1	?	1	1	1	1	1	?	1	1	?	1
16. Protarsomere 4 setal separation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17. Mandible shape	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
18. Lacinia shape	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
19. Lacinia width	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20. Mentum tooth shape	1	0	2	0	0	0	0	0	0	1	2	2	0	0	0	0	0	0	0
21. Mentum tooth emarginate?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22. Mentum tooth bulbous?	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
23. Mentum epilobes	2	2	2	2	2	2	2	2	2	2	0	2	2	1	2	2	2	2	2
24. Pronotal shape	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
25. Pronotal carina	0	0	0	0	0	0	0	0	1	1	1	2	1	1	3	1	0, 1	0	0, 1
26. Metasternum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27. Elytral basal impression	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0, 1	0, 1	0, 1
28. Angulate humeral margin	2	1, 2	1, 2	3	3	3	3	3	3	3	3	3	3	3	3	3	2	1, 2	2
29. Stria 4 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 5. CONTINUED.

Character	ame	bif	che	chp	fus	aep	nra	aen	dur	arz	cnf	scu	crt	cox	rob	prs	str	for	bow
30. Elytra around ed3 and ed5	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
31. Elytral punctures	0	0	0	0	0	0	0	0	0	2	1	2	2	1	0	0	0	0	0
32. Stria 8 depth	1	1	1	2	2	2	2	1	0	1	1	1	1	1	1	0	0	0	0
33. Interval 5 posteriorly	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34. Subapical elytral plica	2	2	2	2	2	2	0	0	2	1	1	2	2	2	2	2	2	2	2
35. Male protarsomere 3 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36. Protarsomere 4 projection	?	3	?	?	?	2	3	3	2	3	3	3	2	2	?	2	2	3	3
Male genitalia																			
Number of specimens	1	3	3	1	1	2	1	2	1	4	4	1	1	3	1	2	2	2	4
37. Flagellar sheath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38. Flagellar sheath sculpture	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39. CSC right lobe	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1
40. CSC right lobe ridge	0	0	0	0	0	0	0	0	2	0	0	0	0	0, 2	0	1, 2	?	1	0
41. VSP dorsal ridge	0	0	0	0	0	0	0	0	3	0	0	0	2	2	0	0	0	0	0
42. VSP dorsal ridge sculpture	2	2	2	2	1	0	0	1	2	0	0	?	0	1	0	2	2	2	0
43. Dark spot on flagellar sheath	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	?	0	0	0
44. Ostial microtrichial patch size	4	4	4	2	1	0	2	4	4	4	4	4	4	4	4	4	4	4	4
45. Ostial scales	—	—	—	0	—	—	—	0	0	1	1	1	—	—	0	0	—	0	—
46. Ostial microtrichial patch	0	0	0	1	0	—	0	1	1	1	1	1	0	0	2	1	0	1	0
47. Ostial sclerotized strip	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	1
48. Ostial strip sculpture	1	1	1	—	—	0	—	—	—	—	—	—	—	—	—	—	?	—	0
49. Pillow with scales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50. Internal sac leftmost central membrane	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
51. Ventral bulge	0, 1	2	1, 2	0	0	0	0	0	0	0, 1	0	0	0	0	0	1	0	0, 1	0
52. Aedeagal apex	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Female genitalia																			
Number of specimens	1	1	1			1		3	1	1	3			3	1	1	2	1	3
53. Vaginal sclerotized plate	0	0	0	?	?	0	?	0	0	0	0	?	?	0	0	0	0	0	0
54. Spermatheca apically indented?	0	0	0	?	?	0	?	0	0	0	0	?	?	0	0	0	0	0	0
55. Stylomere 1 setal length	2	2	2	?	?	1	?	3	2	3	3	?	?	2	1	2	2	2	2
56. Stylomere 2 length	130	200	180	?	?	180	?	110	160	170	190	?	?	195	360	190	190	180	180
57. Number dorsolateral sensilla	2	2	2, 3	?	?	2	?	4, 5	2, 3	3	2, 3	?	?	1–3	3	2	2–4	2, 3	1, 2
58. Sternum X setae	1	1	1	?	?	1	?	1	1	1	1	?	?	1	1	1	1	1	1

TABLE 5. CONTINUED.

Character	ame	bif	che	chp	fus	aep	nra	aen	dur	arz	cnf	scu	crt	cox	rob	prs	str	for	bow
Chromosomes																			
Number of specimens	2	5	1					4		4	7			23			2		7
59. Pairs of autosomes	11	11	11	?	?	?	?	11	?	11	11	?	?	11	?	?	11	?	11
60. Y chromosome size	?	?	?	?	?	?	?	1	?	1	1	?	?	1	?	?	1	?	1
First instar larva																			
Number of specimens			3					1			1			3				2	7
61. Frontale with three spots	?	?	2	?	?	?	?	1	?	?	2	?	?	2	?	?	?	2	2
62. Head (other than spots)	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
63. Frontale behind FR_3	?	?	2	?	?	?	?	0	?	?	2	?	?	2	?	?	?	2	2
64. Frontale: anteriorly behind FR_3	?	?	3	?	?	?	?	0	?	?	3	?	?	3	?	?	?	3	3
65. Parietal eggbursters	?	?	0	?	?	?	?	2	?	?	0	?	?	0	?	?	?	0	0
66. Pronotal microtubercles	?	?	3	?	?	?	?	0	?	?	1	?	?	1	?	?	?	0	0
67. FR_1 width	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
68. FR_3 width	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
69. PR_4 length	?	?	2	?	?	?	?	2	?	?	2	?	?	2	?	?	?	2	2
70. PR_{10} length	?	?	1	?	?	?	?	3	?	?	3	?	?	3	?	?	?	3	3
71. gPR and gME lateral setae	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
72. PR_{13} length	?	?	1	?	?	?	?	1	?	?	1	?	?	1	?	?	?	1	1
73. ME_2 length	?	?	2	?	?	?	?	3	?	?	3	?	?	3	?	?	?	3	3
74. ME_{14} length	?	?	3	?	?	?	?	3	?	?	3	?	?	3	?	?	?	3	3
75. TE_6 length	?	?	1	?	?	?	?	2	?	?	2	?	?	2	?	?	?	2	2
76. TE_{11} length	?	?	2	?	?	?	?	2	?	?	2	?	?	2	?	?	?	2	2
77. TE_{11} shape	?	?	1	?	?	?	?	1	?	?	1	?	?	1	?	?	?	1	1
78. TE_α	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
79. EP_1 length	?	?	1	?	?	?	?	1	?	?	1	?	?	1	?	?	?	1	1
80. Segment VIII EP_1 width	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
81. Seta ST_2 on segment IX	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
82. Mandible mesal margin	?	?	0	?	?	?	?	1	?	?	1	?	?	0	?	?	?	0	0
Second instar larva																			
Number of specimens								1			1			1				1	
83. Extra setae near FR_3	?	?	?	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	?
84. L2 stipites	?	?	?	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	?
85. Long urogomphus setae	?	?	?	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	?

Table 6. Character states of *Bracteon* fossils. The two Columbia Bridge specimens are from an early Holocene, late Pleistocene locality from Vermont. The other specimens are from the Miocene Beaufort Formation. Lot number JVM 3-73 is from Banks Island; all the rest are from Meighen Island. Numbers in front of characters are those from Table 2. For numbered characters, state code matches those in Table 2; for others, code as follows: **body part**: E = elytron, P = pronotum; **3rd interval width**: W = distinctly wider than 2nd, N = as wide as second; **ed5 pit shape**: C = circular. "?" symbolizes missing data.

	Lot number and *Specimen number*													
	Columbia Bridge		**JVM 3-73**						**JVM 5-73**		**MRA 8-3-75-1**	**MRA 8-1-75-4**		
Character	*A1*	*A2*	*B2*	*B3*	*B4*	*B5*	*B6*	*B7*	*B3*	*B5*	*B4*	*A4*	*A5*	*B5*
Body part	E	E	E	E	E	E	E	E	E	P	E	P	P	E
1. Silver spots	1	?	1	1	1	1	1	1	1	?	1	?	?	1
2. Mirrors on 3rd?	3	?	3	3	3	?	?	0	3	?	3	?	?	3
3. Mirrors on 4th and 5th?	?	?	3	3	3	?	?	0	3	?	?	?	?	3
7. Sculpticell shape	0	?	0	0	0	0	0	0	0	?	0	?	?	0
9. Midlateral setae	?	?	?	?	?	?	?	?	?	1	?	1	1	?
10. ed3/5 and stria	0	0	0	0	0	0	0	0	0	?	0	?	?	?
11. ed3/5 and silver spot	1	?	0	0	0	0	0	?	0	?	0	?	?	0
25. Pronotal carina	?	?	?	?	?	?	?	?	?	1	?	0	1	?
28. Humeral margin	2	1	?	1	2	?	1	?	?	?	2	?	?	?
29. Stria 4 straight?	0	0	0	0	0	0	0	?	?	?	0	?	?	?
Interval 3 width	W	?	W	W	W	W	W	W	W	?	W	?	?	W
ed5 pit shape	?	?	?	?	?	?	?	C	?	?	?	?	?	?

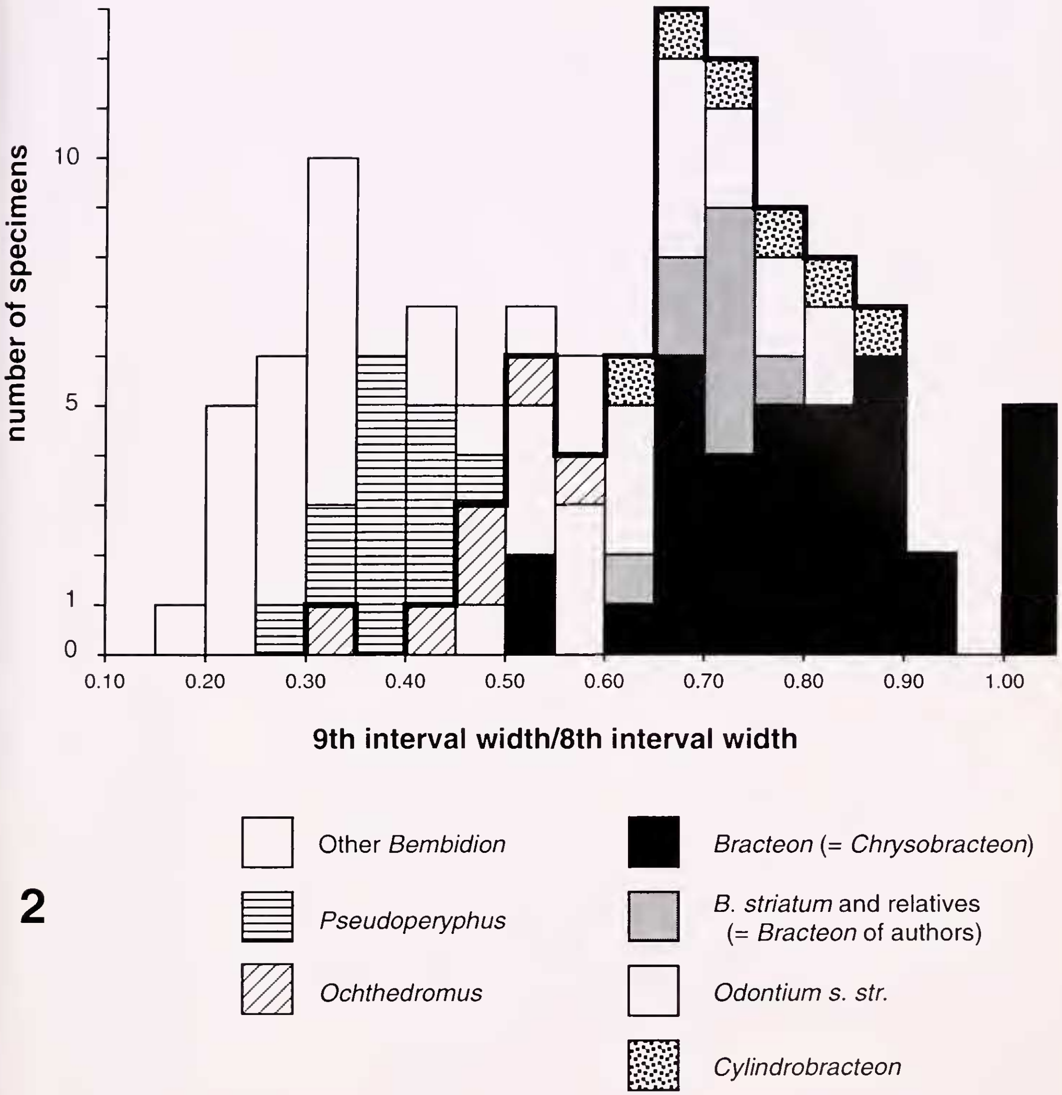

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Figure 2. Histogram of ratio (interval 9 width)/(interval 8 width) of studied *Bembidion* species. Two or three specimens measured of most species. Included are all *Bembidion* species of Tables 2, 4, and 5. Results for *Odontium* subgeneric group members are enclosed by a thick black line. The divisions between *Odontium*, *Cylindrobracteon*, and the *B. striatum* group are those recognized by Netolitzky (1942) and Lindroth (1962); note that I include all three within subgenus *Odontium* (see discussion in text).

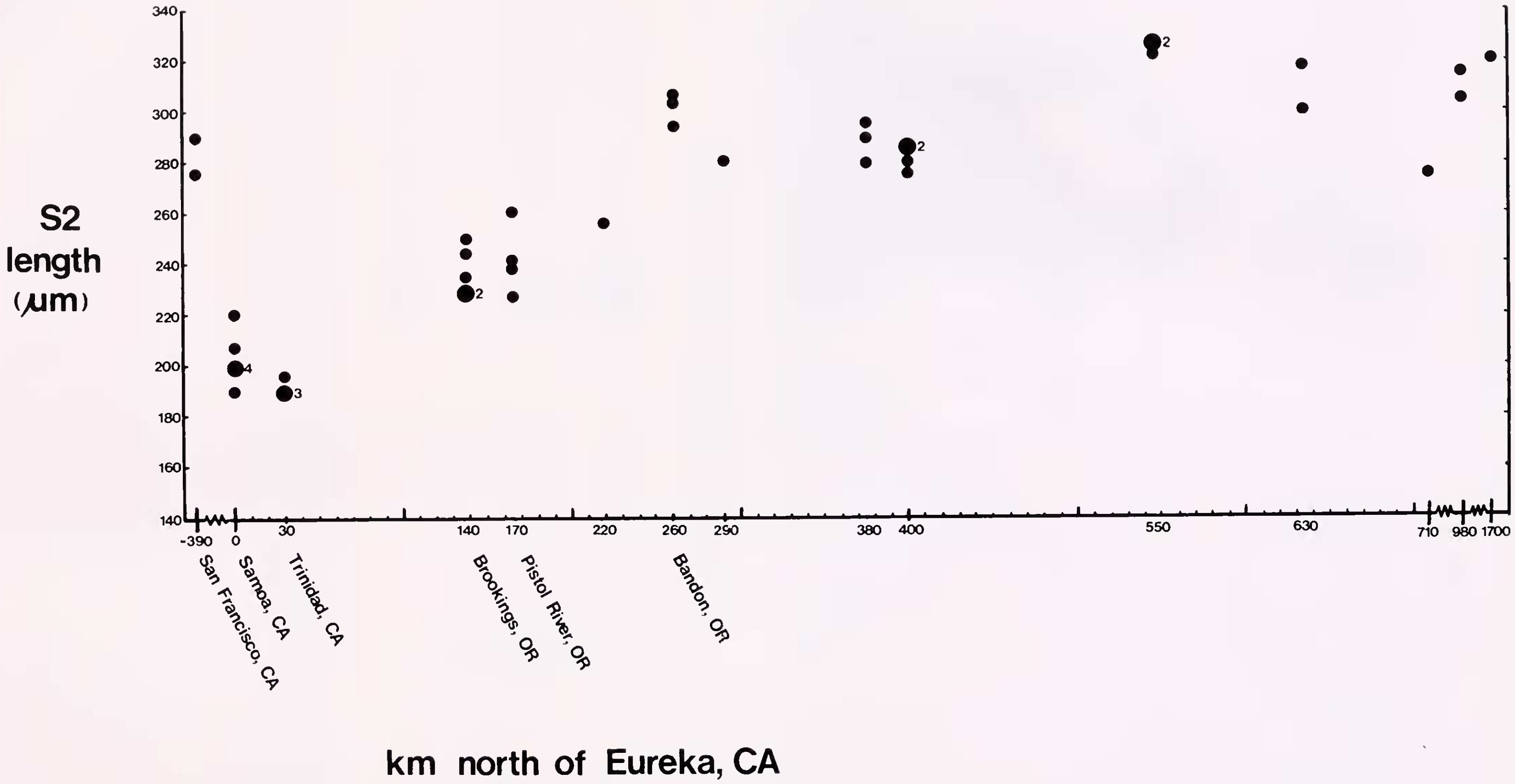


Figure 3. Geographic variation of *B. zephyrum* female second stylomere length.

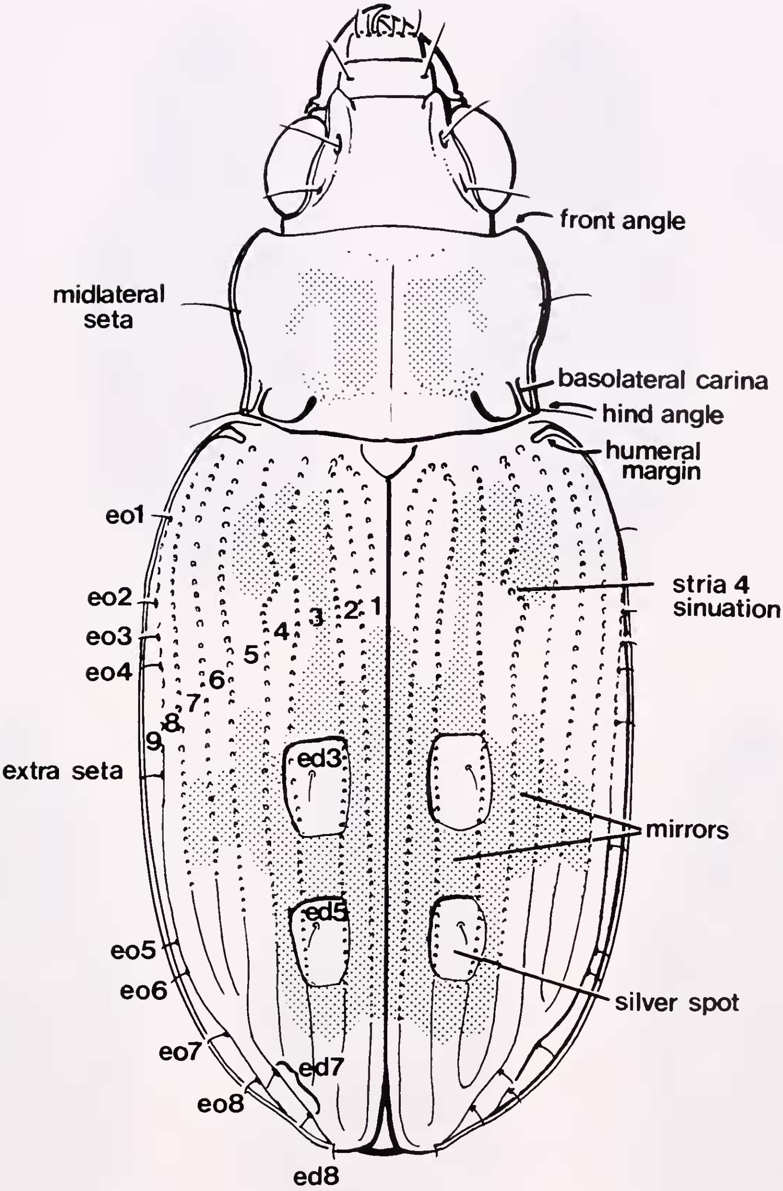
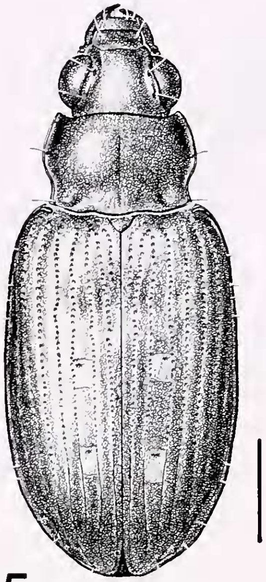


Figure 4. Diagrammatic dorsal view of imaginary *Bracteon* adult illustrating structures and terms. Elytral setal codes (eo1, ed3, and so on) follow nomenclature of Erwin and Kavanaugh (1981). Note that in *Bracteon*, there is either one or (as shown) two setae in the ed7 area. Transverse basal impression of elytron is located at stria 4 sinuation. Elytral intervals are numbered.



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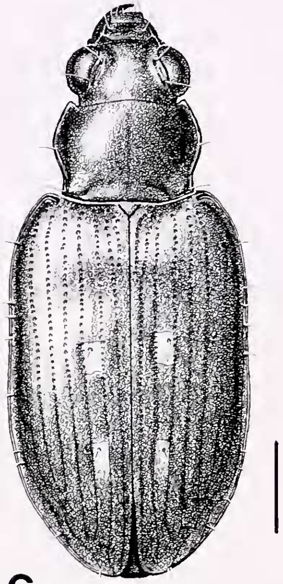

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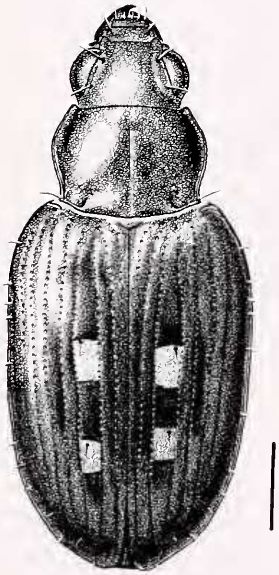

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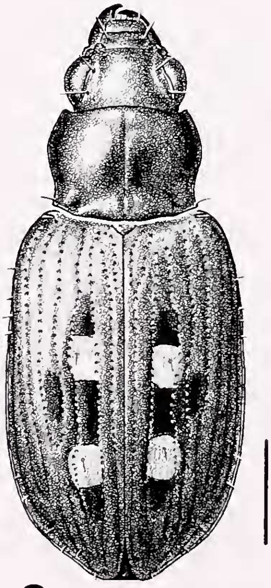

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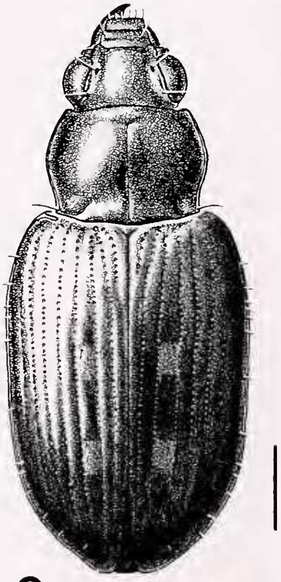

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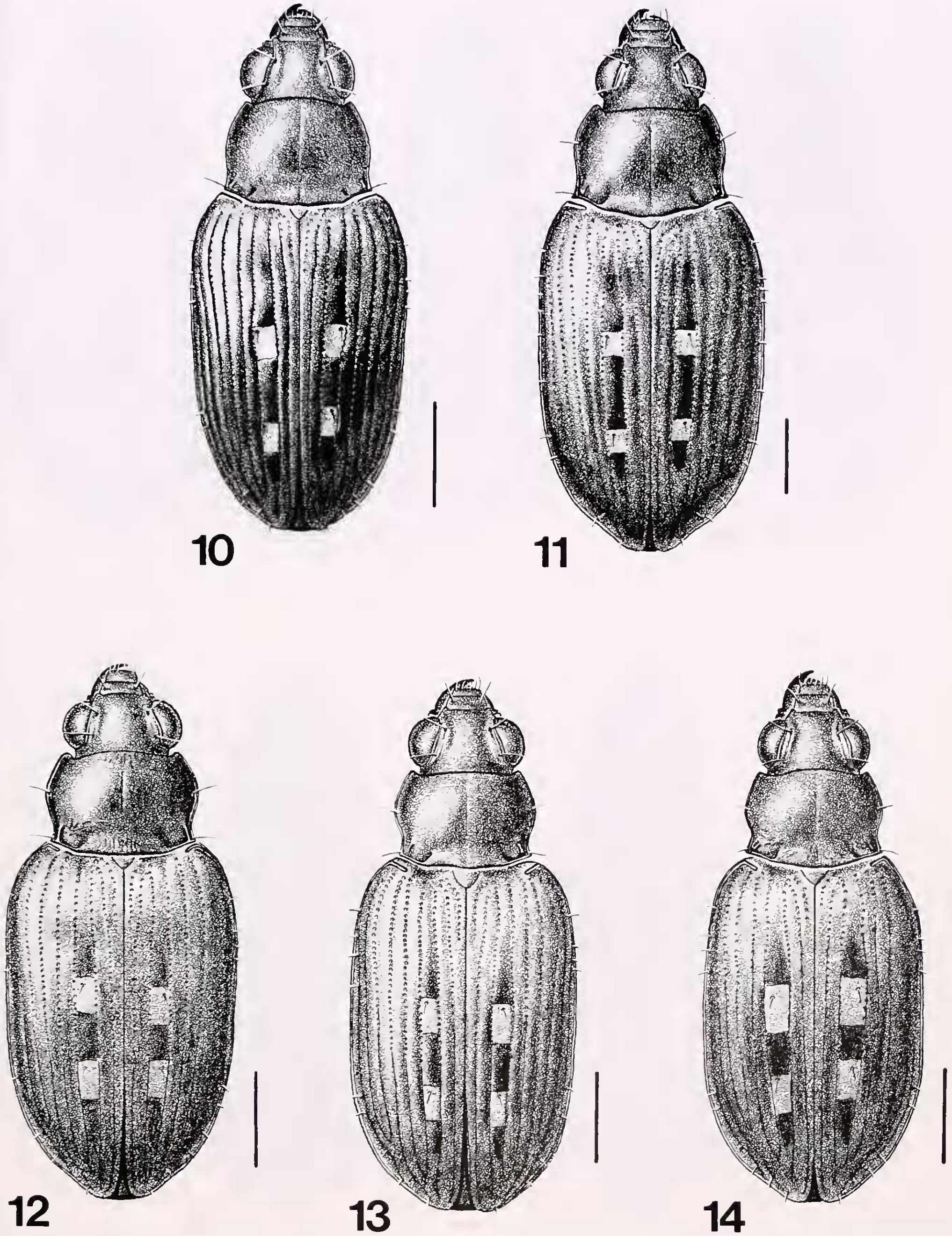
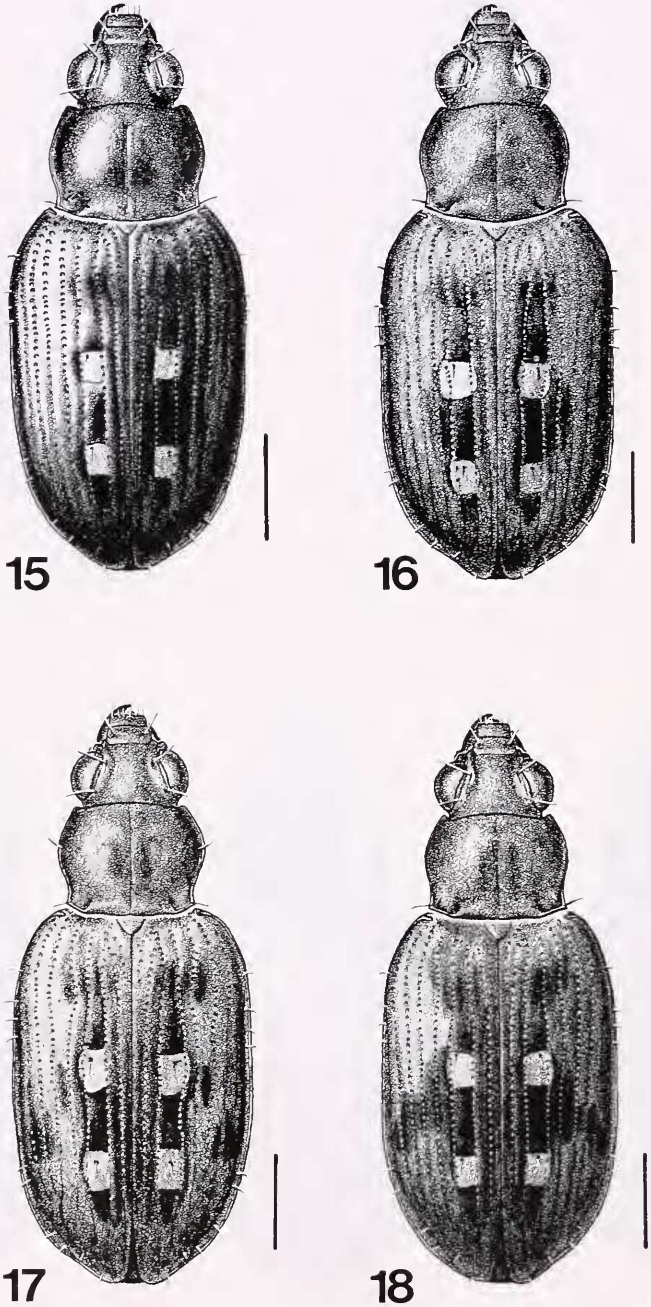
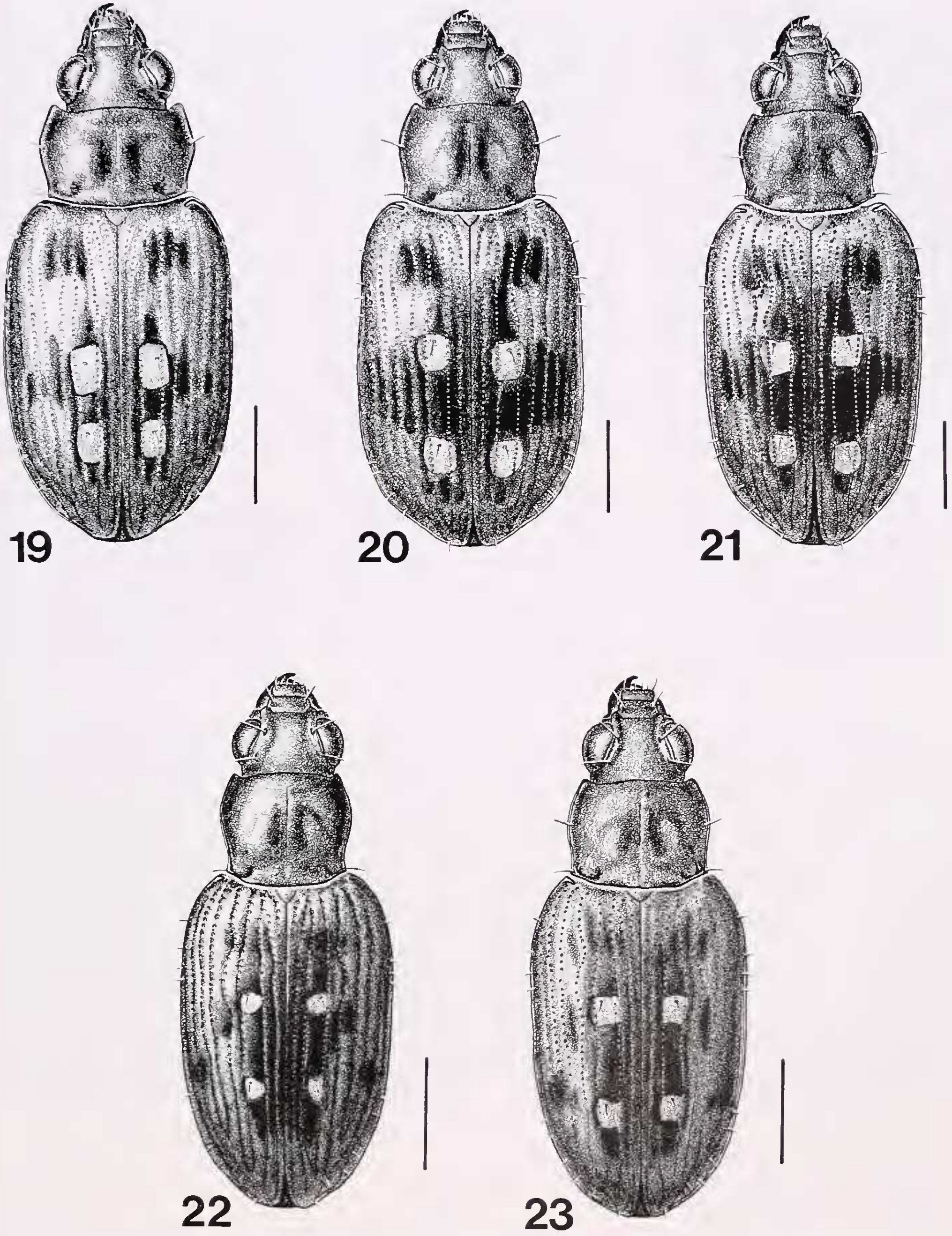
Figures 5–9. Dorsal view of adult male *Bracteon;* appendages omitted. Scale bars = 1 mm. 5. *B. balli* (Maymont, Saskatchewan). 6. *B. foveum* (Frenchman Butte, Saskatchewan). 7. *B. argenteolum* (Mora, Sweden). 8. *B. alaskense* (Lake Brooks, Alaska). 9. *B. semenovi* (Black Irtysh R., Russia)



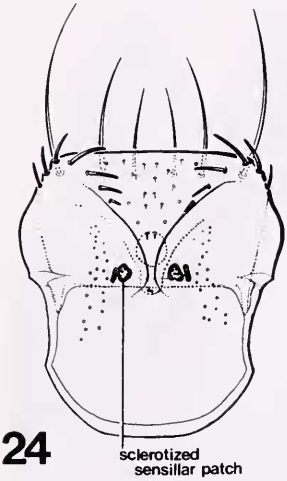
Figures 10–14. Dorsal view of adult male *Bracteon;* appendages omitted. Scale bars = 1 mm. 10. *B. stenoderum* (Kyoto, Japan). 11. *B. punctatostriatum* (Spring Creek Basin, Alberta). 12. *B. carinula* (North Saskatchewan River north of Lloydminster, Saskatchewan). 13. *B. velox* (Irtysh R., Russia). 14. *B. lapponicum* (Old Crow, Yukon).



Figures 15–18. Dorsal view of adult male *Bracteon;* appendages omitted. Scale bars = 1 mm. 15. *B. hesperium* (Van Zandt, Washington). 16. *B. lorquinii* (Lockwood, Nevada). 17. *B. litorale* (Emsdetten, Germany). 18. *B. conicolle* (Ulan-Baator, Mongolian Peoples' Republic).



Figures 19–23. Dorsal view of adult male *Bracteon;* appendages omitted. Scale bars = 1 mm. 19. *B. zephyrum* (Waldport, Oregon). 20. *B. levettei levettei* (Brocket, Alberta). 21. *B. levettei carrianum* (Paynton, Saskatchewan). 22. *B. inaequale* (Listowel, Ontario). 23. *B. inaequale* (Van Zandt, Washington).



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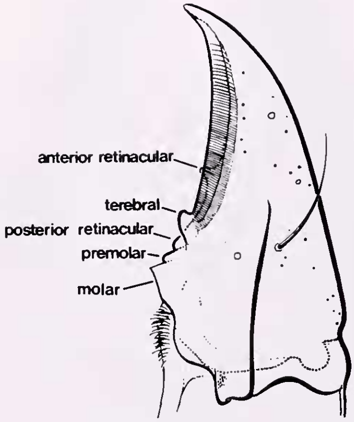

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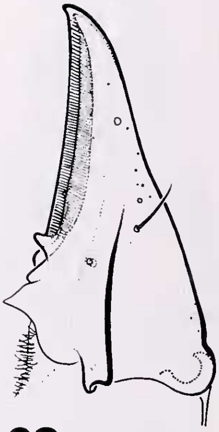

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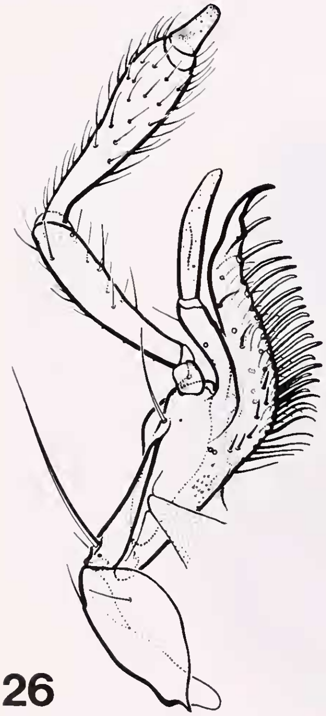

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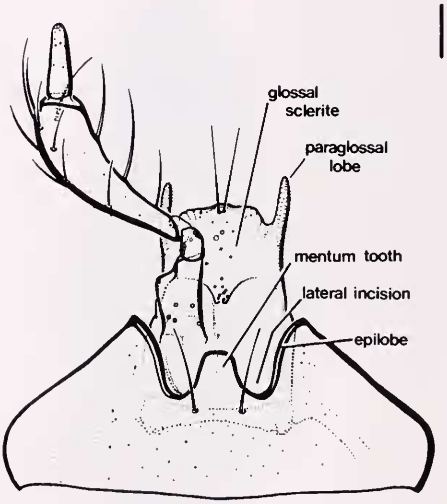

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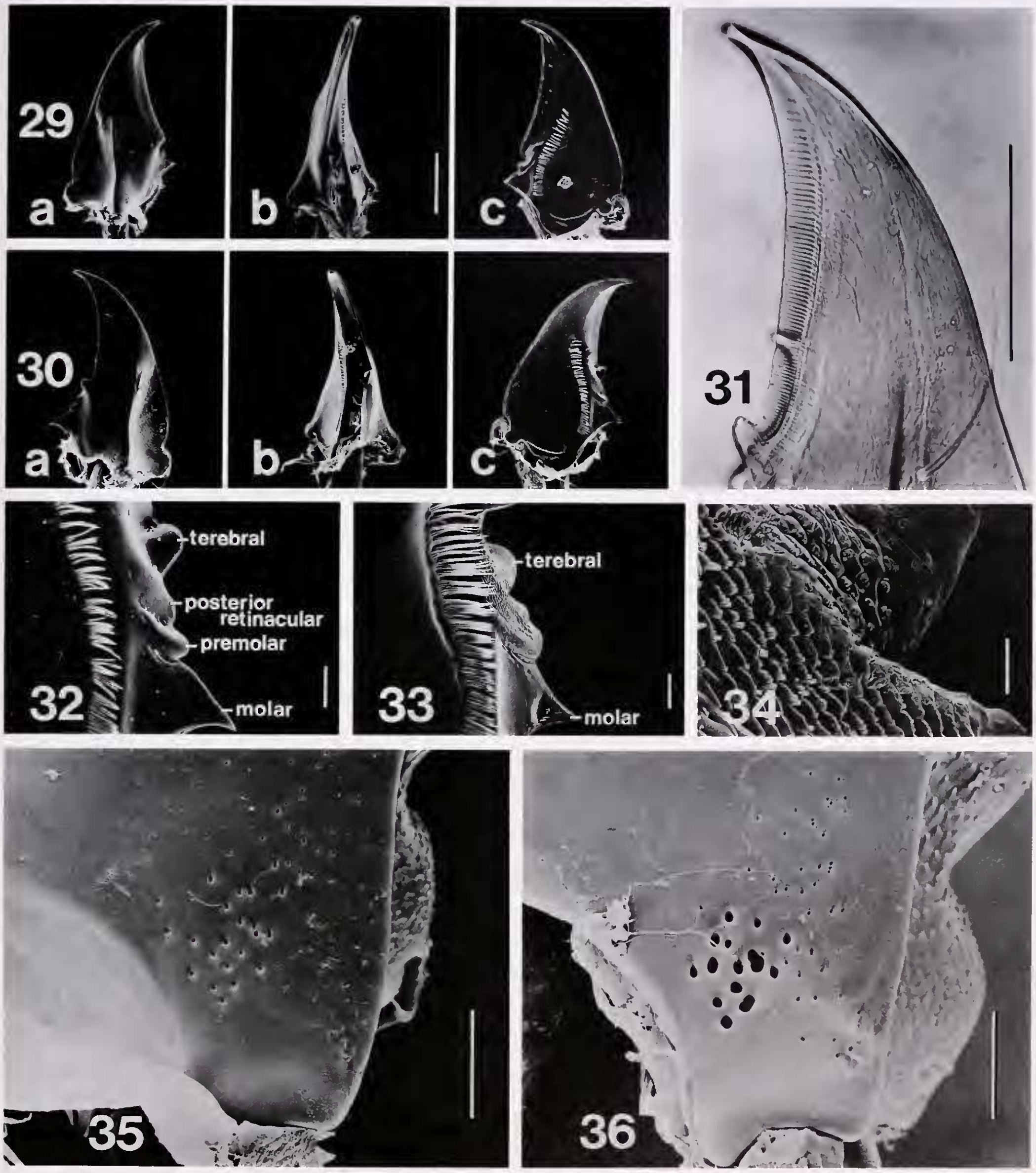
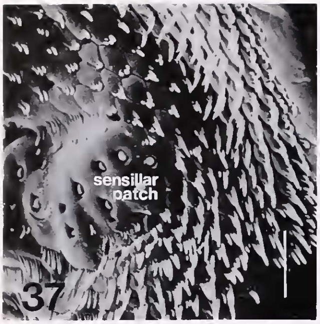
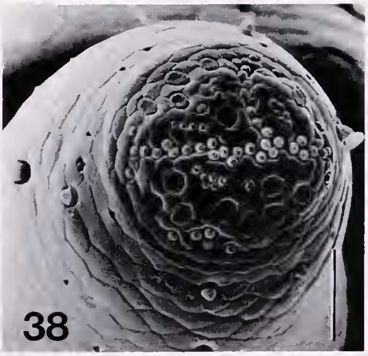
Figures 24–27. Cleared mouthpart structures of adult *B. foveum*. All figures at same scale; scale bar = 100 μm. 24. Ventral view of labrum. 25. Dorsal view of right mandible. 26. Ventral view of right maxilla. 27. Ventral view of mentum, ligula, and right labial palpus.

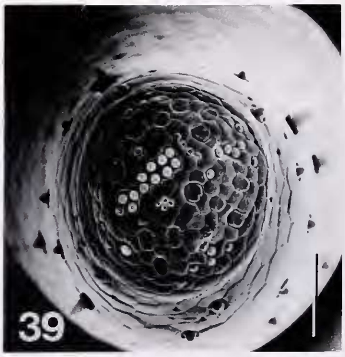
Figure 28. Dorsal view of cleared right mandible of *B. confusum*. Same scale as Figures 24–27.

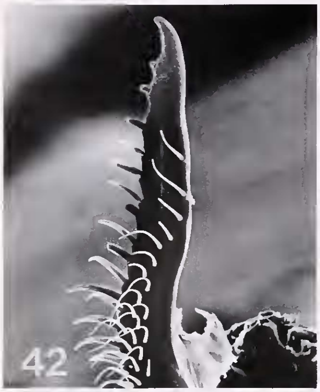


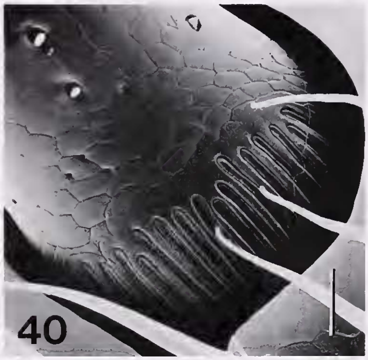
Figures 29–36. Mandibles of *Bracteon*. 29. Left mandible of *B. foveum*. Scale bar = 200 μm. (**a.** Dorsal view. **b.** Mesal view. **c.** Ventral view.) 30. Right mandible of *B. foveum*. Scale bar = 200 μm. (**a.** Dorsal view. **b.** Mesal view. **c.** Ventral view.) 31. Cleared right mandible of *B. foveum*, showing mesal pore canals. Scale bar = 200 μm. 32. Basal mesal edge of right mandible of *B. foveum*, ventral view. Scale bar = 40 μm. 33. Basal mesal edge of right mandible of *B. punctatostriatum*, ventral view. Scale bar = 40 μm. 34. Microsculpture around terebral tooth of right mandible of *B. punctatostriatum*. Scale bar = 10 μm. 35. Dorsal surface of right mandible of *B. balli*, near dorsal condyle. Scale bar = 40 μm. 36. Dorsal surface of right mandible of *B. foveum*, near dorsal condyle. Scale bar = 40 μm.

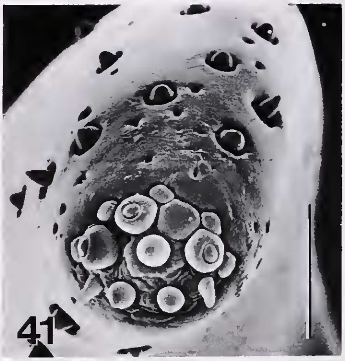


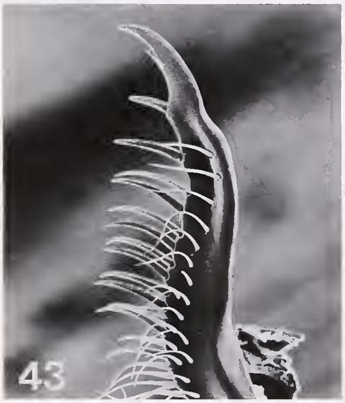


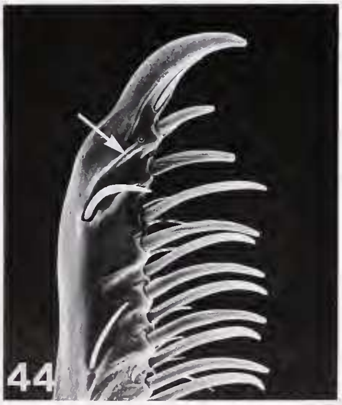


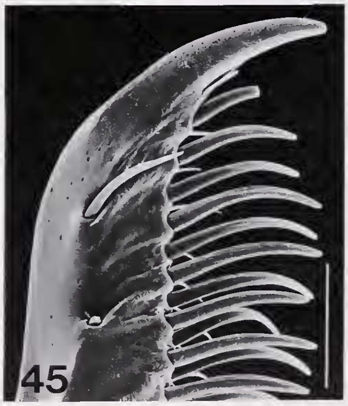


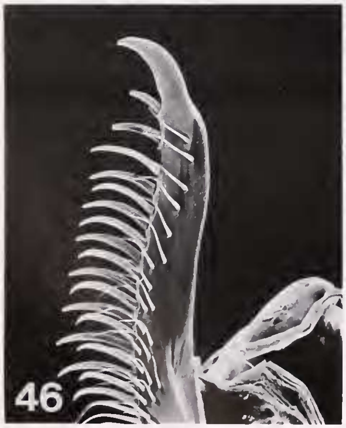


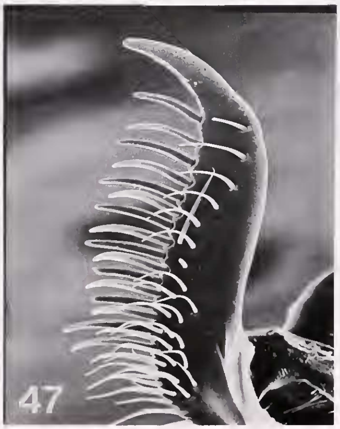


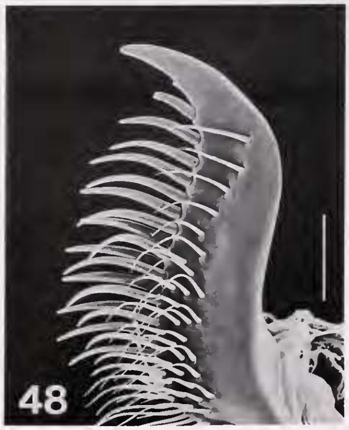




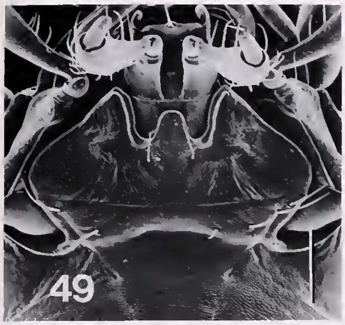








Figures 37–41. Mouthpart sensilla of adult *Bracteon*. Scale bars = 10 μm. 37. Epipharynx of *B. foveum*, right side near epipharyngeal hump, ventral view. 38. Apex of maxillary palp of *B. foveum*. 39. Apex of labial palp of *B. foveum*. 40. Digitiform sensilla at base of maxillary palp of *B. balli*. 41. Apex of galea of *B. foveum*.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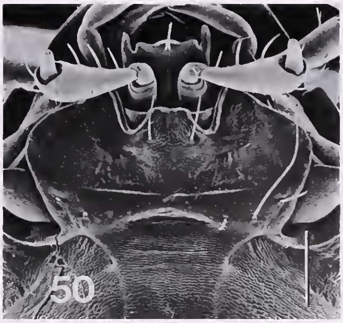
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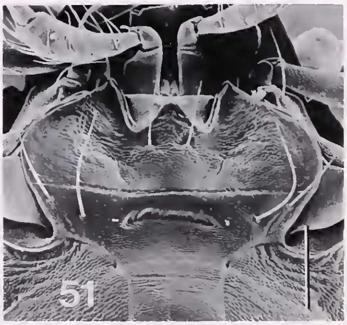
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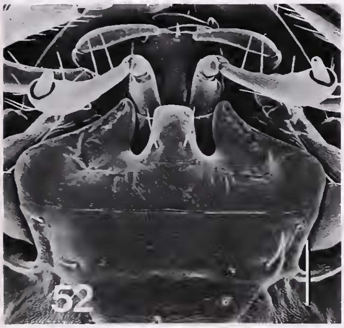
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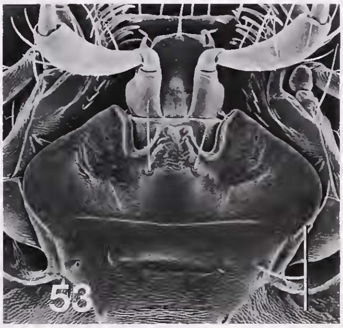
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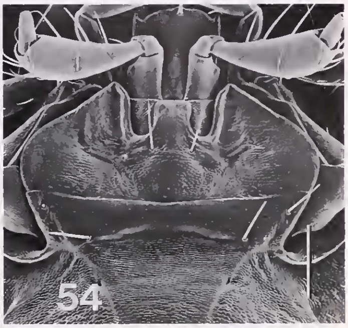
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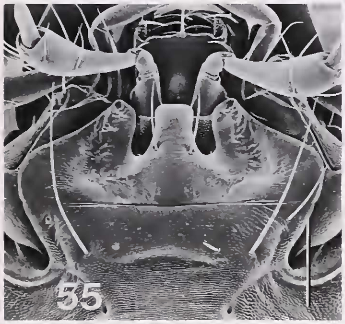
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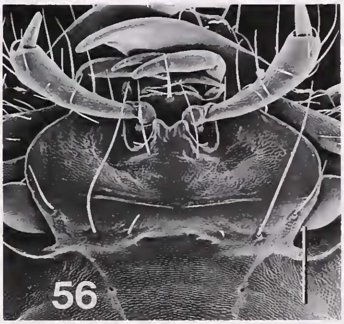
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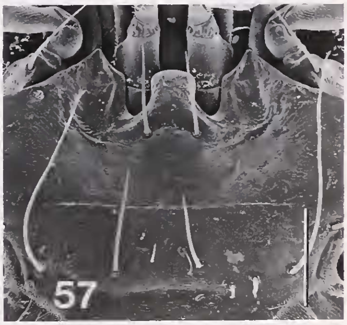
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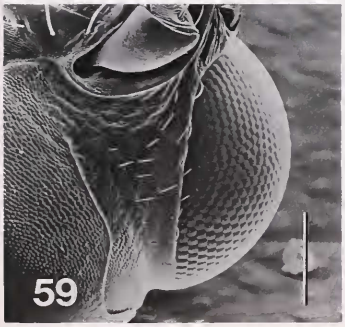
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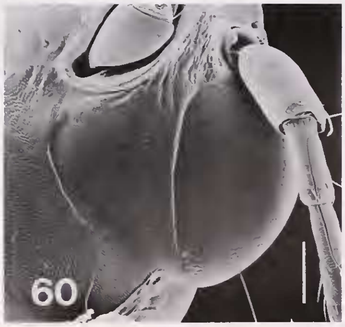
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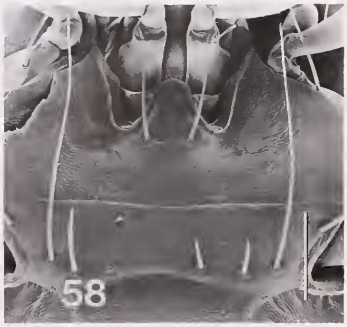
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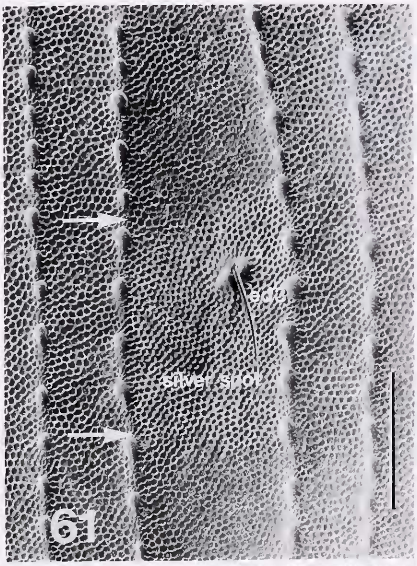
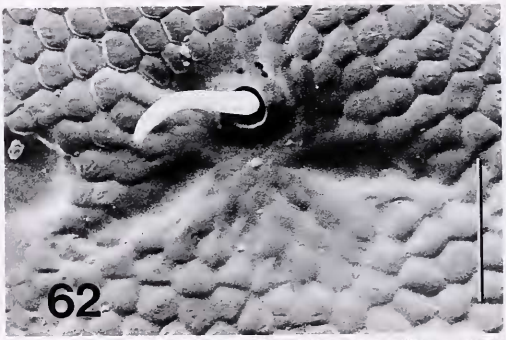
Figures 49–58. Menta of *Bembidion* adults, ventral view. Scale bars = 200 μm. 49. *B. balli.* 50. *B. alaskense.* 51. *B. lapponicum.* 52. *B. punctatostriatum.* 53. *B. hesperium.* 54. *B. zephyrum.* 55. *B. levettei carrianum.* 56. *B. litorale.* 57. *B. bifossulatum cheyennense.* 58. *B. bifossulatum bifossulatum.*

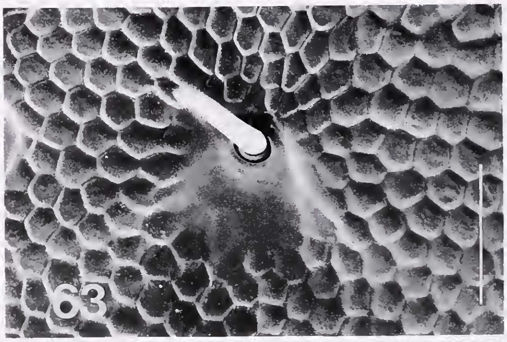
Figures 59–60. Lateroventral views of *Bracteon* heads. Scale bars = 200 μm. 59. *B. lapponicum.* 60. *B. punctatostriatum.*

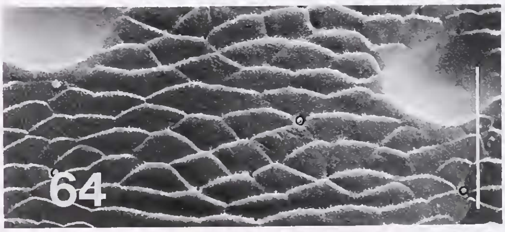
⟵

Figures 42–48. Right laciniae of *Bembidion.* Scale bars = 100 μm. 42. *B. confusum,* dorsal view. 43. *B. bowditchii,* dorsal view. 44. *B. lapponicum,* ventral view. Note subapical ridge (arrow). 45. *B. punctatostriatum,* ventral view. 46. *B. lapponicum,* dorsal view. 47. *B. alaskense,* dorsal view. 48. *B. punctatostriatum,* dorsal view.

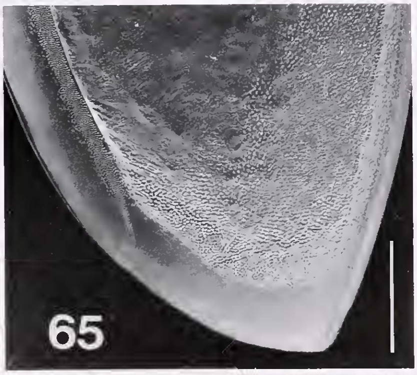


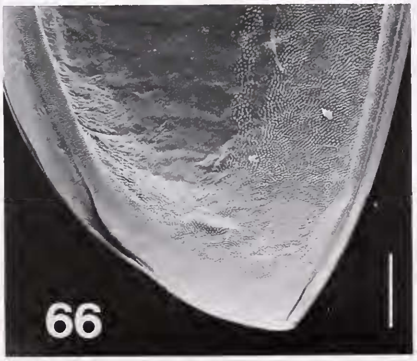


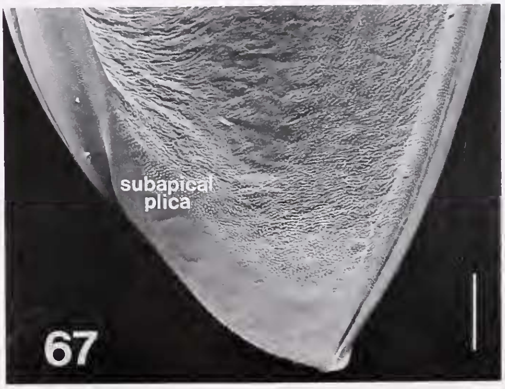




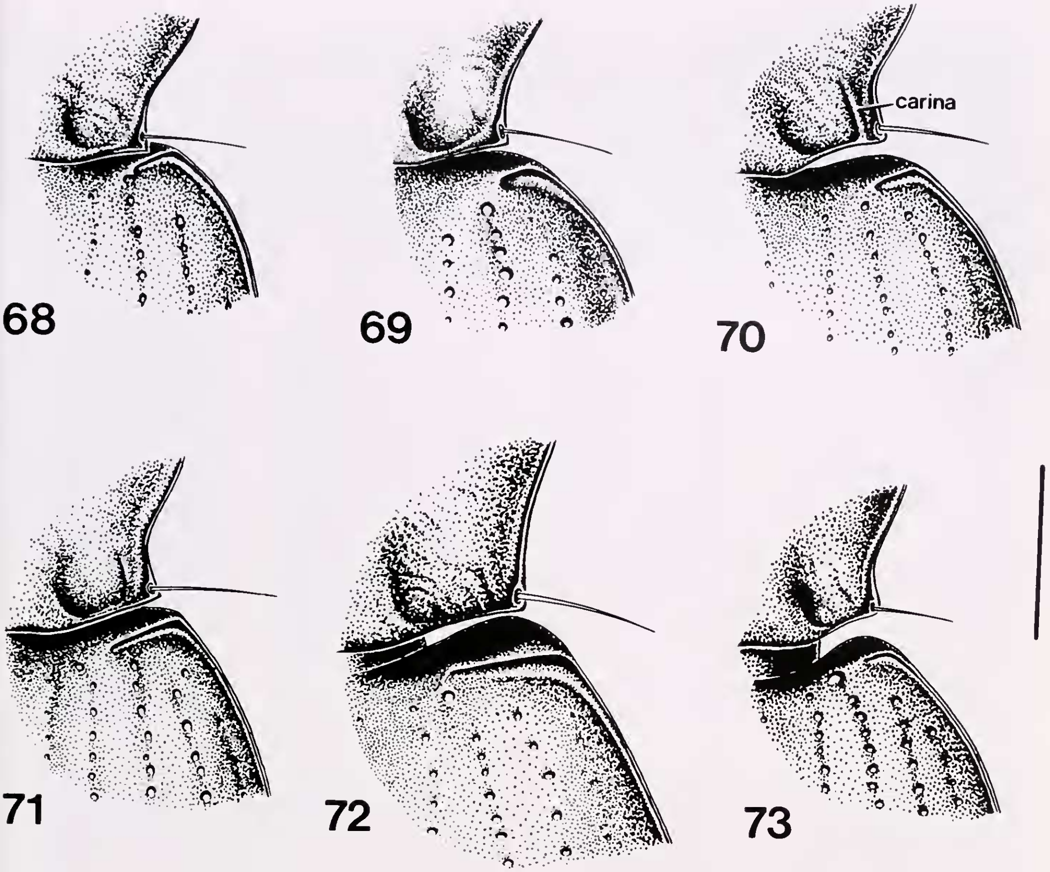
Figures 61–64. Elytral structure, dorsal surface. 61. Right elytron, *B. lapponicum*, around seta ed3. Arrows indicate anterior and posterior limits of silver spot. Scale bar = 200 μm. 62. *B. balli*, microsculpture around seta ed3 in silver spot of elytron. Scale bar = 40 μm. 63. *B. foveum*, microsculpture around seta ed3 in silver spot of elytron. Scale bar = 40 μm. 64. *B. hesperium* male, microsculpture of elytron in interval 6. Scale bar = 40 μm.

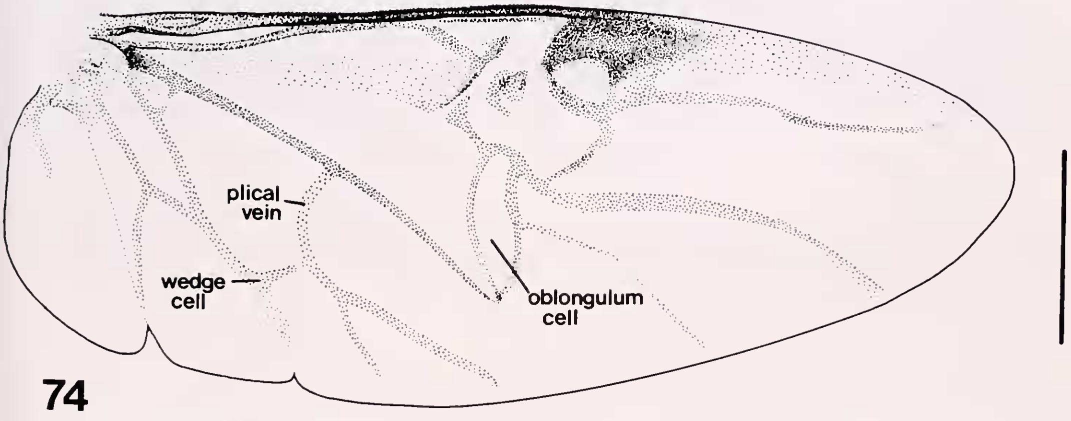






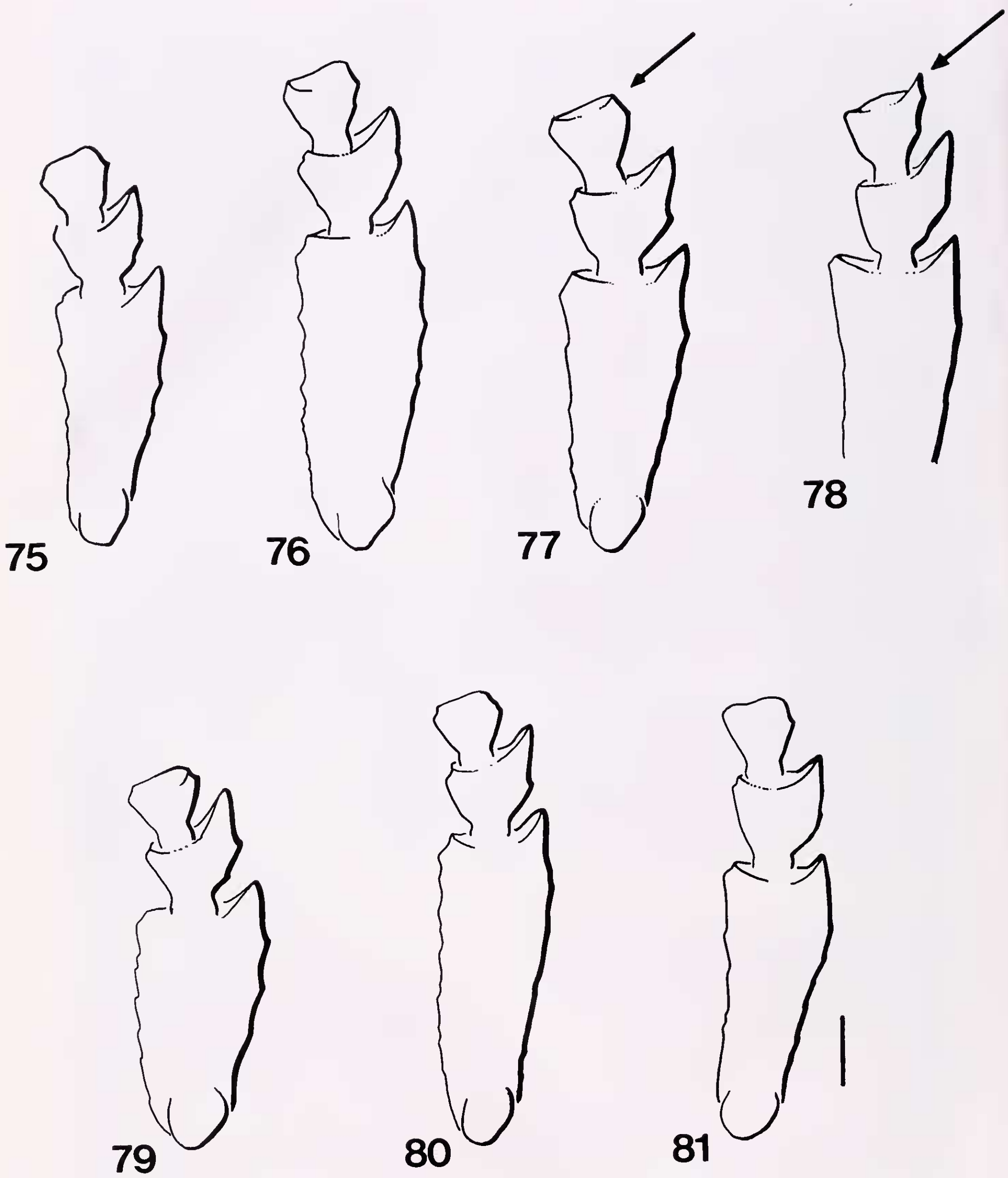
Figures 65–67. Ventral surface of elytral apex, showing subapical plica. Scale bars = 200 μm. 65. *B. aenulum*. 66. *B. confusum*. 67. *B. punctatostriatum*.



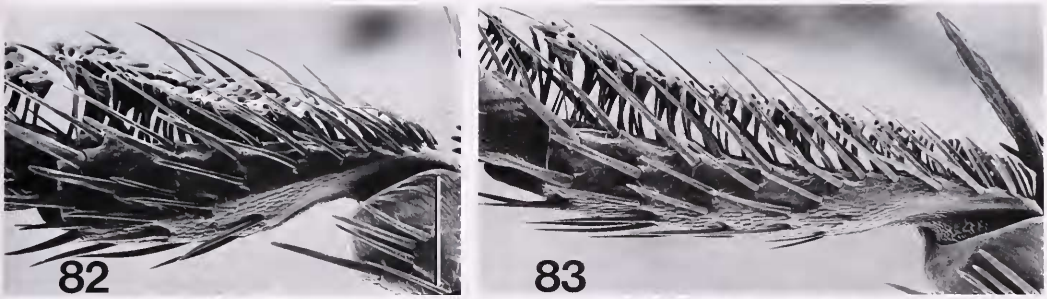


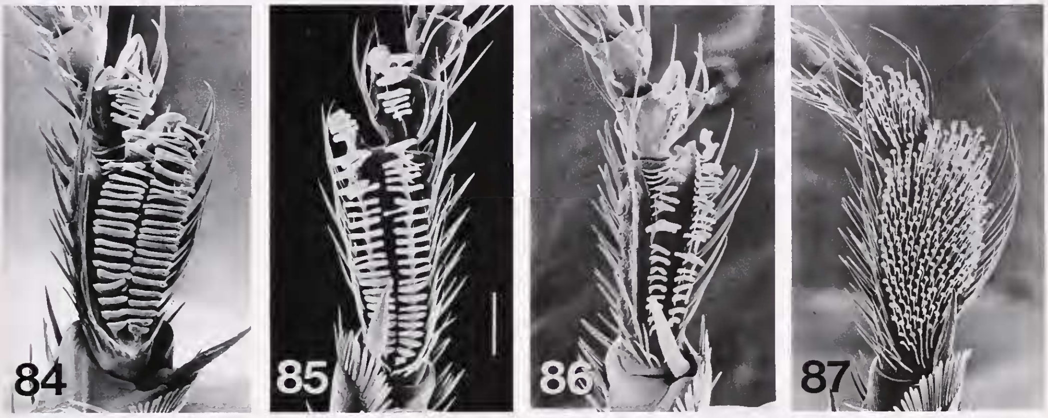
Figures 68–73. Shoulder region of *Bracteon*. Scale bar = 0.5 mm. 68. *B. balli*. 69. *B. foveum*. 70. *B. carinula*. 71. *B. lapponicum*. 72. *B. punctatostriatum*. 73. *B. inaequale*.

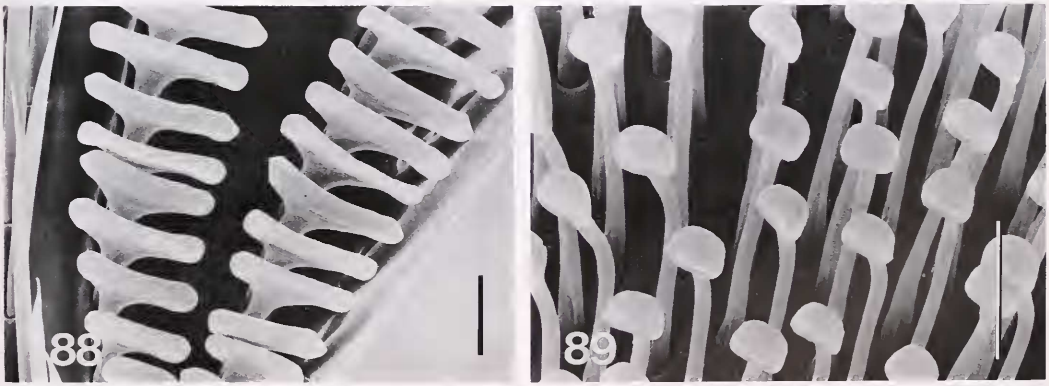
Figure 74. Right metathoracic wing of *B. inaequale*. Scale bar = 1 mm.



Figures 75–81. First three male left protarsomeres of *Bracteon*, dorsal view. Scale bar = 100 μm. 75. *B. balli*. 76. *B. foveum*. 77. *B. argenteolum*. Note lack of lateroapical projection on protarsomere 3. 78. *B. semenovi*. Note lateroapical projection on protarsomere 3. 79. *B. zephyrum*. 80. *B. levettei levettei*. 81. *B. litorale*.



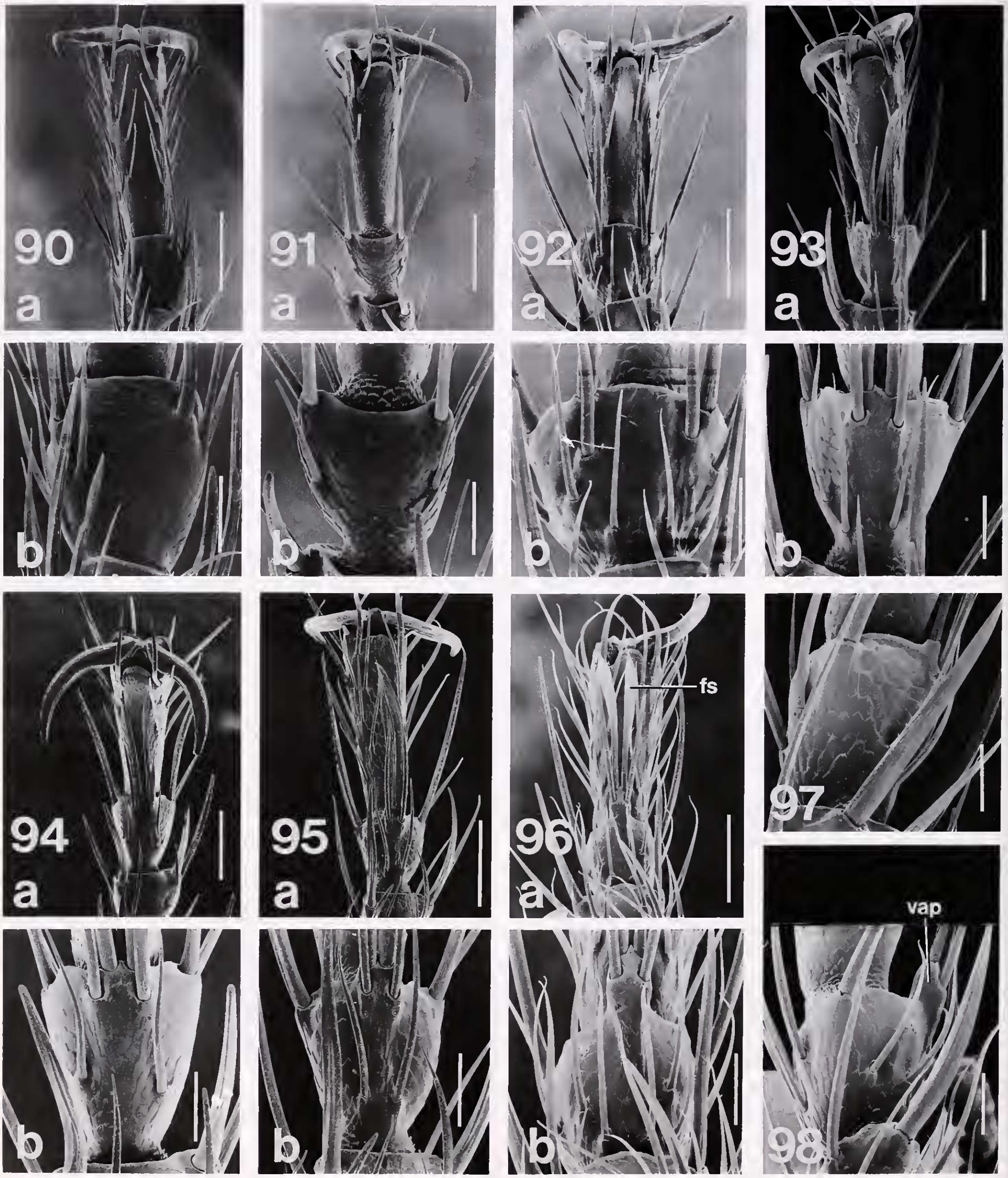




Figures 82, 83. Lateral view of male protarsomere 1. Scale bar = 100 μm; 82. *B. zephyrum*. 83. *B. levettei levettei*.

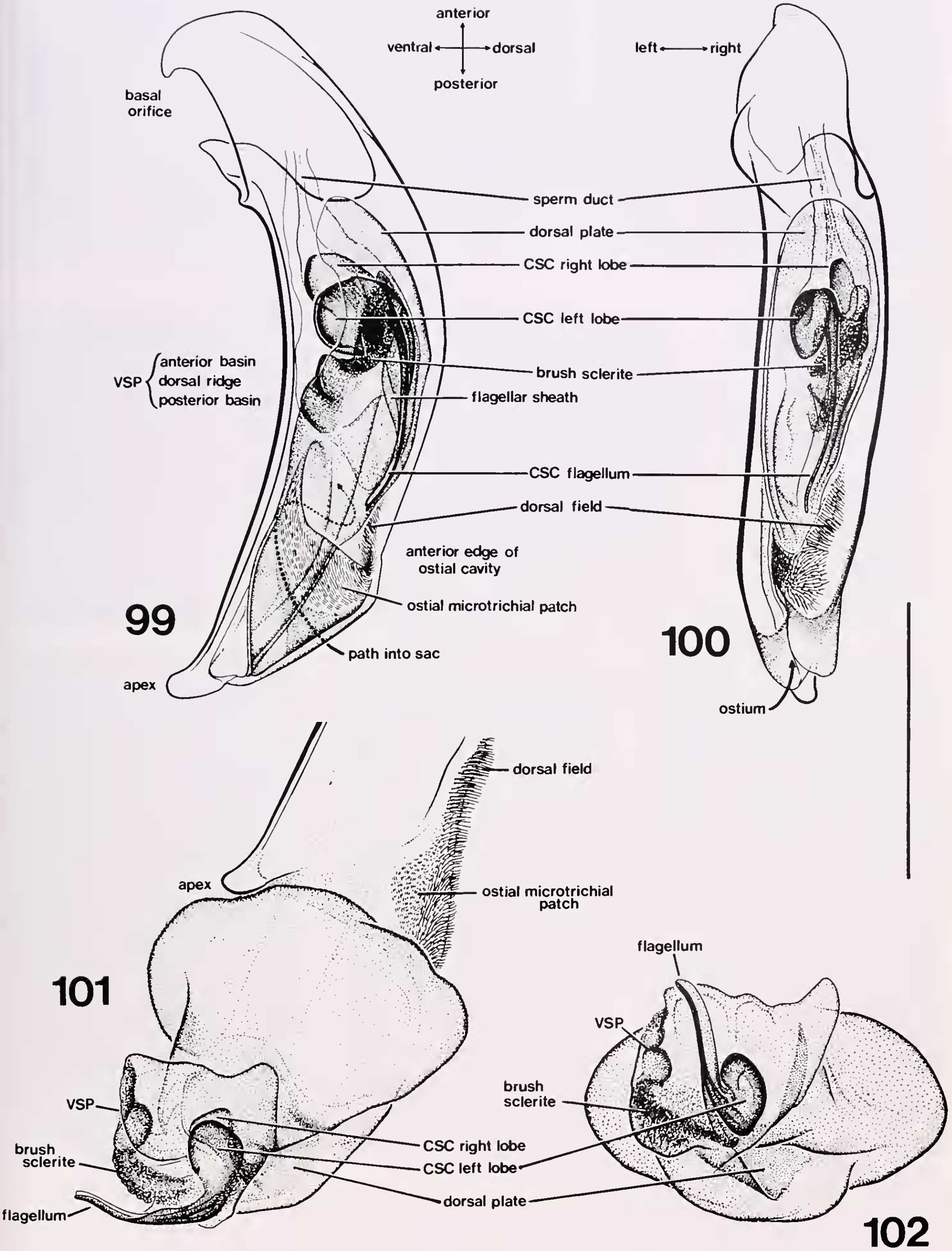
Figures 84–87. Ventral view of male protarsus. Scale bar = 100 μm. 84. *B. zephyrum*. 85. *B. levettei carrianum*. 86. *B. conicolle*. 87. *Asaphidion alaskanum*.

Figures 88, 89. Ventral view of male protarsomere 1, showing adhesive setae. Scale bars = 20 μm. 88. *B. argenteolum*. 89. *Asaphidion alaskanum*.

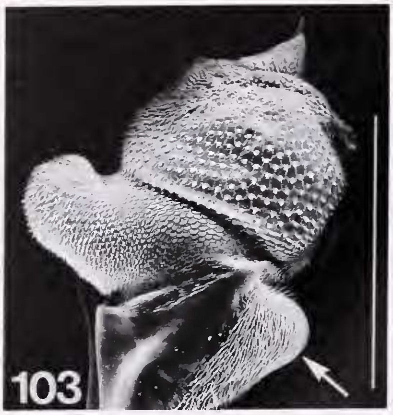


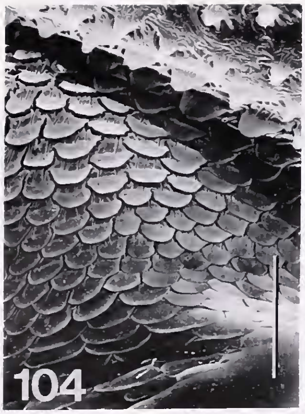
Figures 90–96. Ventral view of male protarsomeres. **a**: protarsomeres 4 and 5; scale bars = 100 μm. **b**: protarsomere 4; scale bars = 40 μm. 90. *Asaphidion alaskanum*. 91. *Bembidion interventor*. 92. *B. alaskense*. 93. *B. argenteolum*. 94. *B. punctatostriatum*. 95. *B. hesperium*. 96. *B. balli*. fs: flattened ventroapical setae of protarsomere 4.

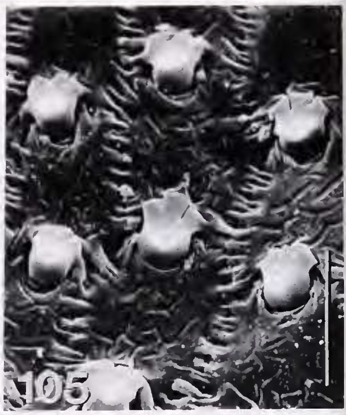
Figures 97, 98. Lateral view of male protarsomere 4. Scale bars = 40 μm. 97. *B. argenteolum*. 98. *B. balli*. vap: ventroapical projection.

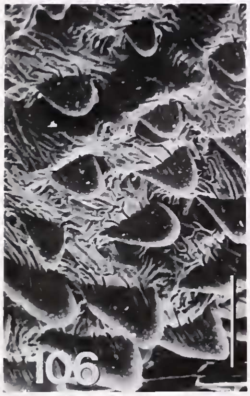


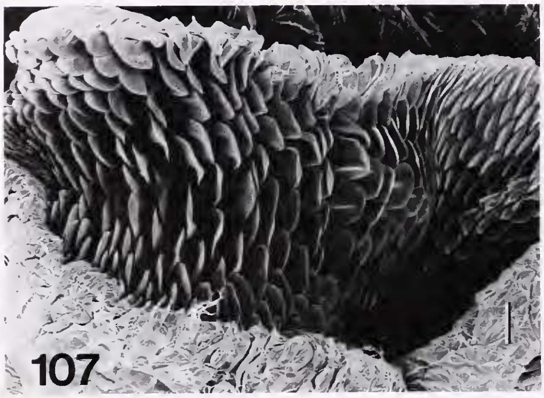
Figures 99–102. Median lobe of male aedeagus of *B. balli;* most membrane microsculpture omitted. Scale bar = 0.5 mm. 99. Left lateral view of median lobe, internal sac inverted. 100. Dorsal view of median lobe, internal sac inverted. 101. Left lateral view of everted internal sac. 102. Apex of everted internal sac.

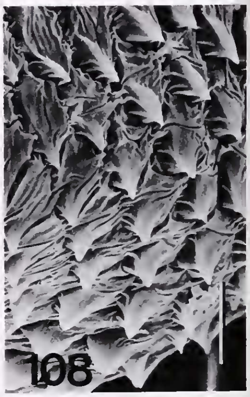


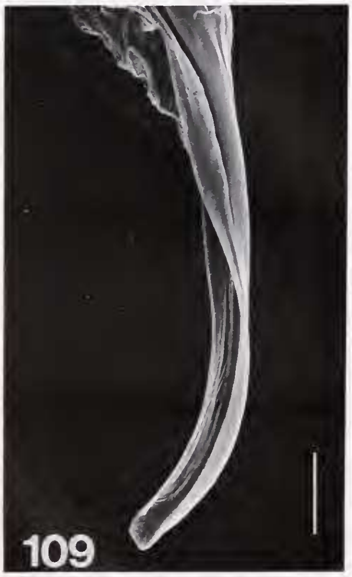


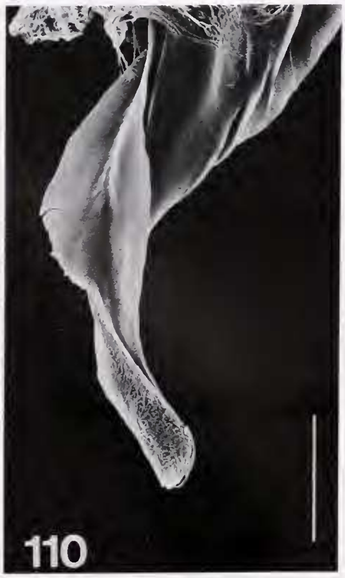


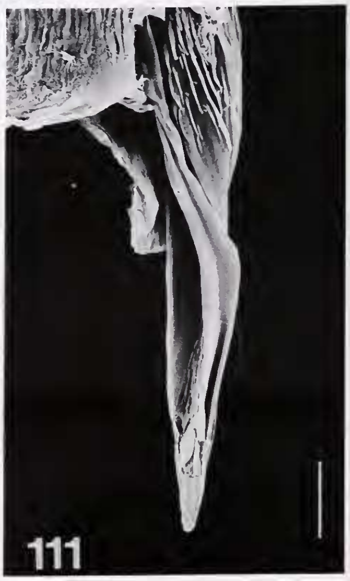






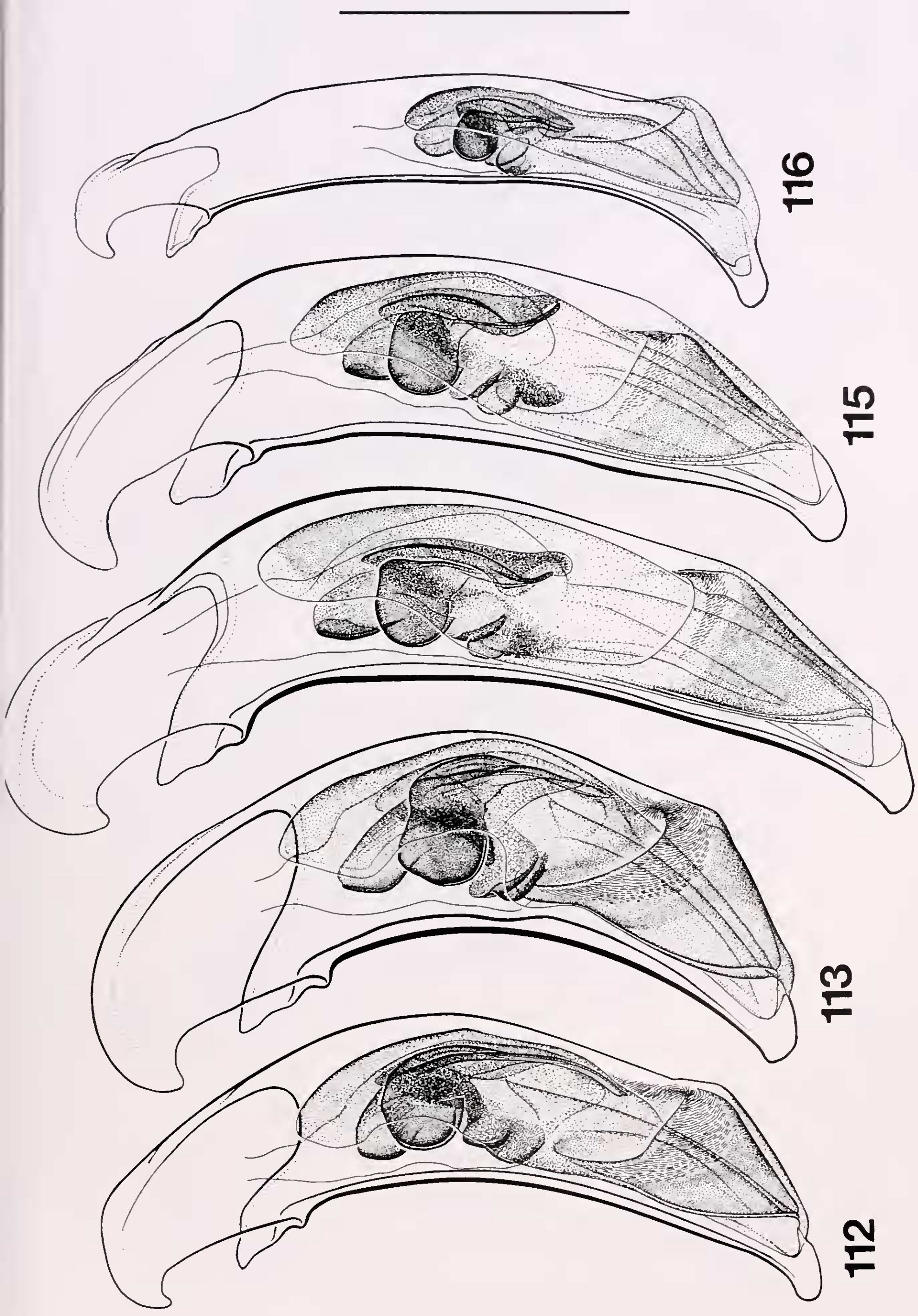




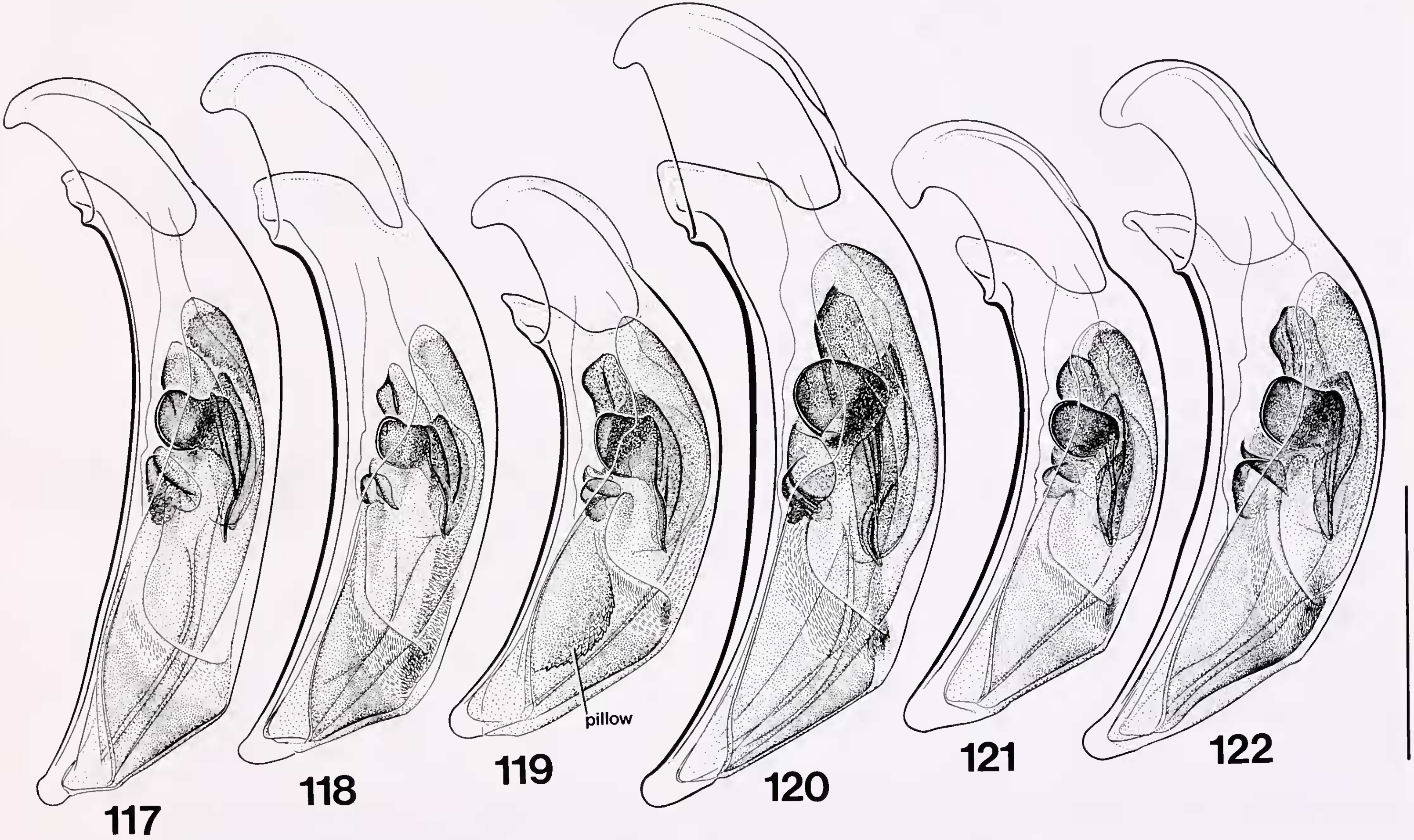


Figures 103–108. Internal sac microsculpture. 103. Everted internal sac of *B. levettei carrianum*, left lateral view. Arrow indicates basodorsal lobe. Scale bar = 500 μm. 104. Everted internal sac of *B. levettei carrianum*, microsculpture on left lateral face near ostial flag. Scale bar = 50 μm. 105. Everted internal sac of *B. levettei carrianum*, microsculpture on left lateral face. Scale bar = 20 μm. 106. Everted internal sac of *B. levettei carrianum*, microsculpture on right lateral face. Scale bar = 20 μm. 107. Everted internal sac of *B. bifossulatum cheyennense*, showing brush sclerite. Scale bar = 20 μm. 108. Everted internal sac of *B. chalceum*, showing large scales. Scale bar = 20 μm.

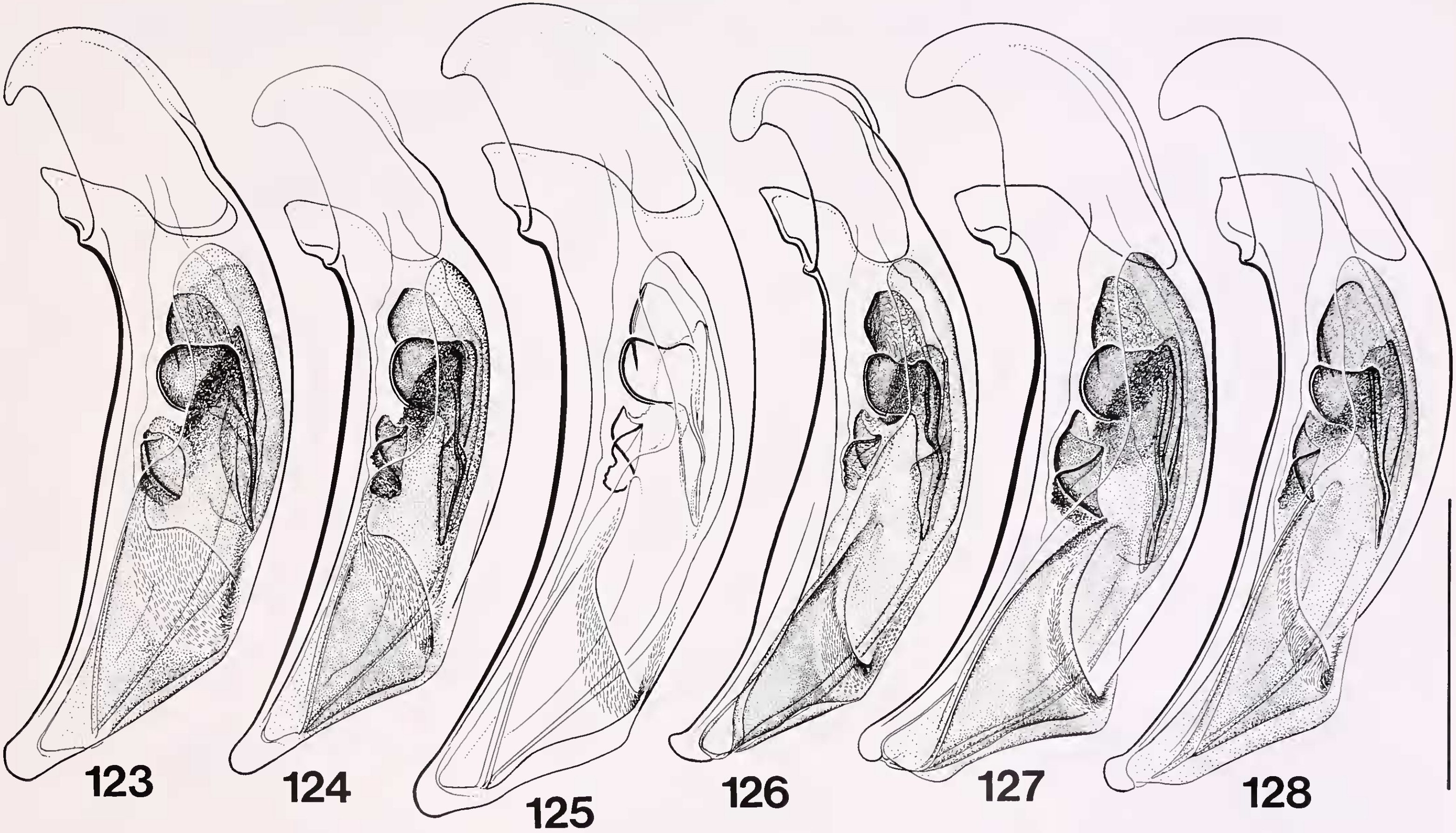
Figures 109–111. Left lateral view of flagella of *Bracteon*. View slightly more ventral than in Figures 129–144. Scale bars = 40 μm. 109. *B. balli*. 110. *B. alaskense*. 111. *B. levettei carrianum*.



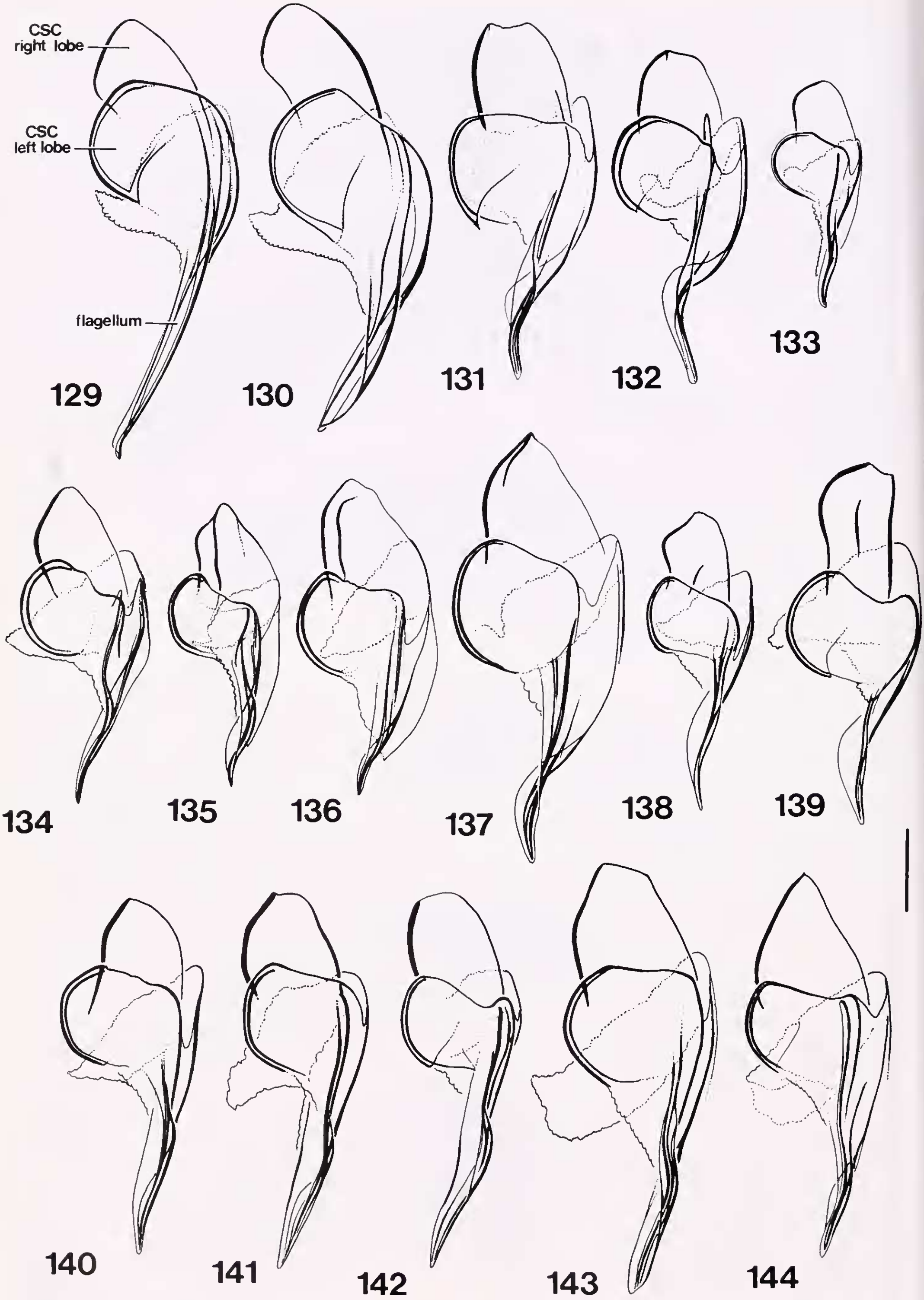
Figures 112–116. Median lobe of aedeagus, left lateral view. Scale bar = 0.5 mm. 112. *B. balli.* 113. *B. foveum.* 114. *B. argenteolum.* 115. *B. alaskense.* 116. *B. stenoderum.*



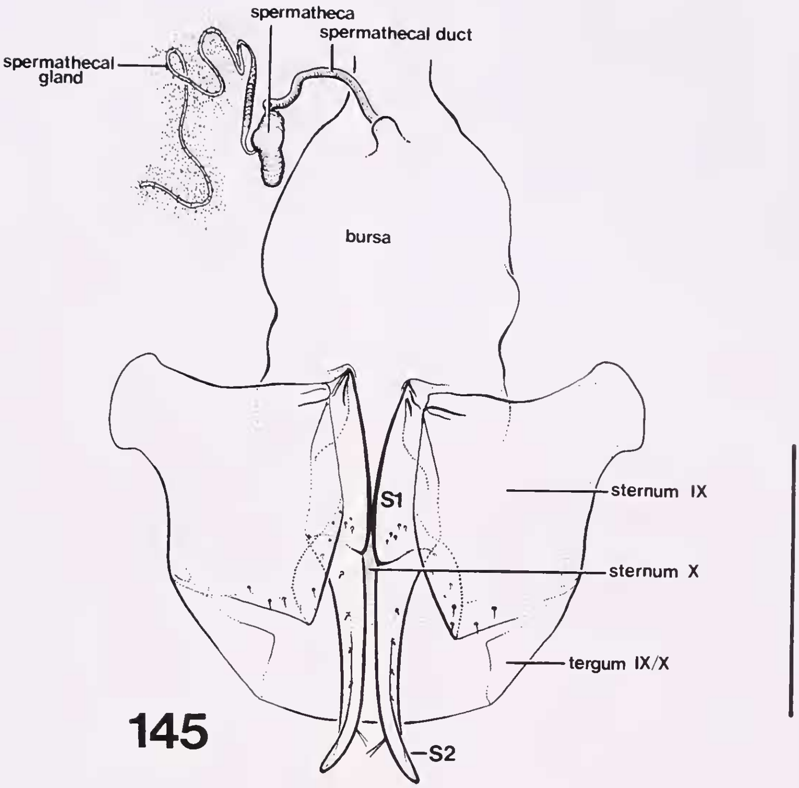
Figures 117–122. Median lobe of aedeagus, left lateral view. Scale bar = 0.5 mm. 117. *B. carinula*. 118. *B. velox*. 119. *B. lapponicum*. 120. *B. punctatostriatum*. 121. *B. hesperium*. 122. *B. lorquinii*.



Figures 123–128. Median lobe of aedeagus, left lateral view. Scale bar = 0.5 mm. 123. *B. zephyrum*. 124. *B. levettei carrianum*. 125. *B. levettei levettei*. 126. *B. inaequale*. 127. *B. litorale*. 128. *B. conicolle*.



Figures 129–144. Central sclerite complex of male internal sac, with outline of brush sclerite, left lateral view. Scale bar = 100 µm. 129. *B. balli*. 130. *B. foveum*. 131. *B. argenteolum*. 132. *B. alaskense*. 133. *B. stenoderum*. 134. *B. carinula*. 135. *B. velox*. 136. *B. lapponicum*. 137. *B. punctatostriatum*. 138. *B. hesperium*. 139. *B. lorquinii*. 140. *B. zephyrum*. 141. *B. levettei carrianum*. 142. *B. inaequale*. 143. *B. litorale*. 144. *B. conicolle*.



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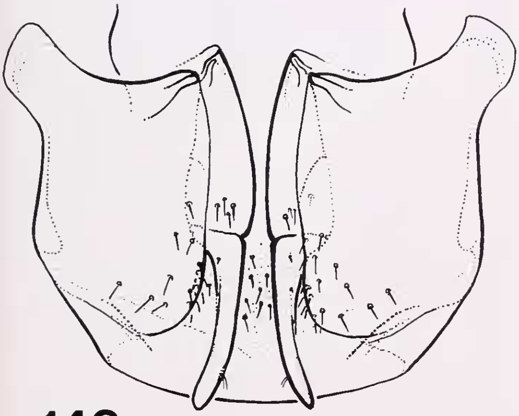

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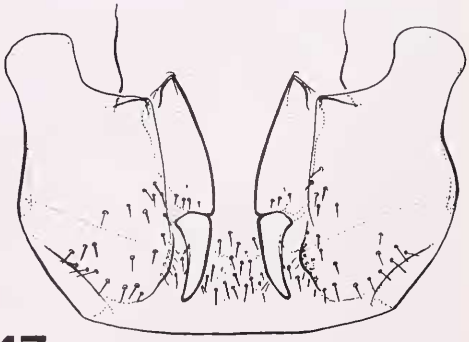
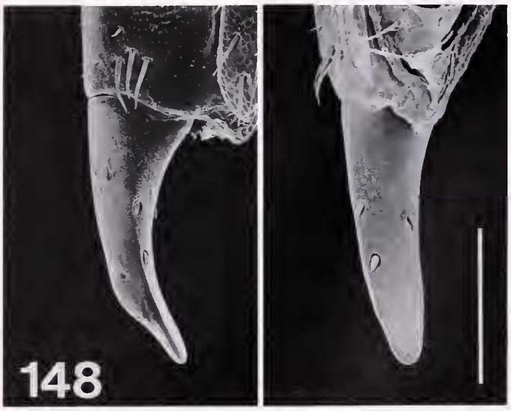


147

Figures 145–147. Ventral view of cleared, inverted female genitalia. Scale bar = 0.5 mm. 145. *B. carinula.* 146. *B. alaskense.* 147. *B. balli.*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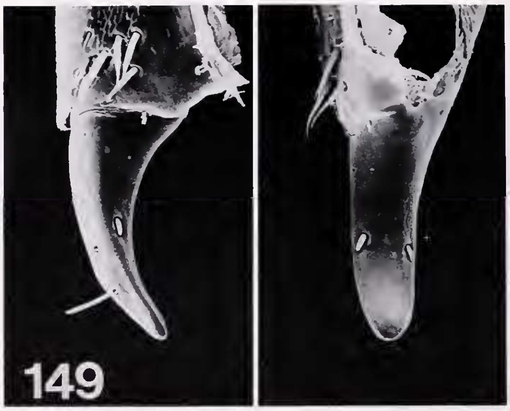
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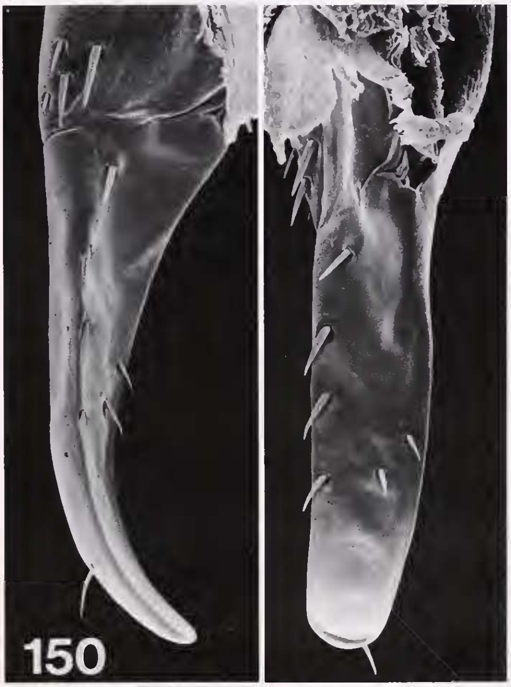
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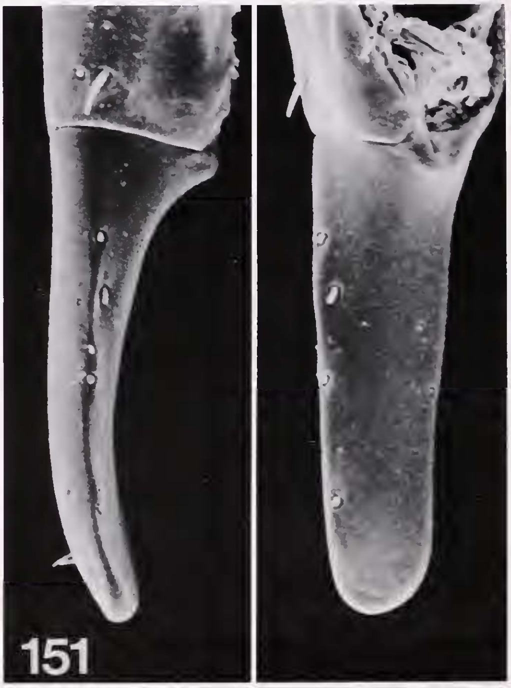
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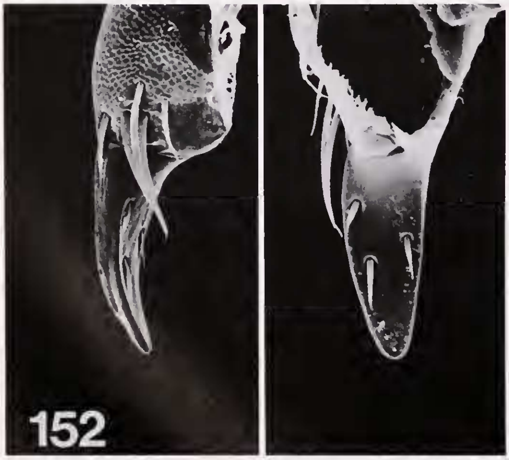
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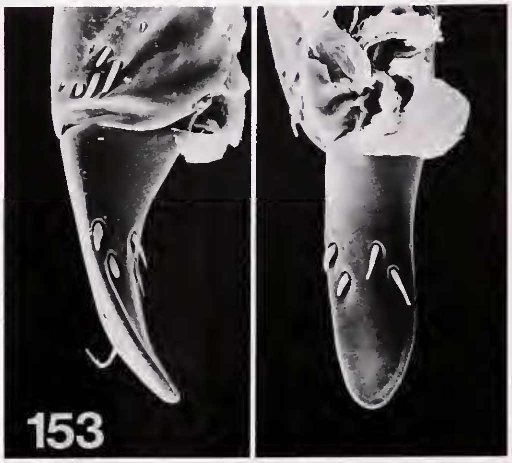
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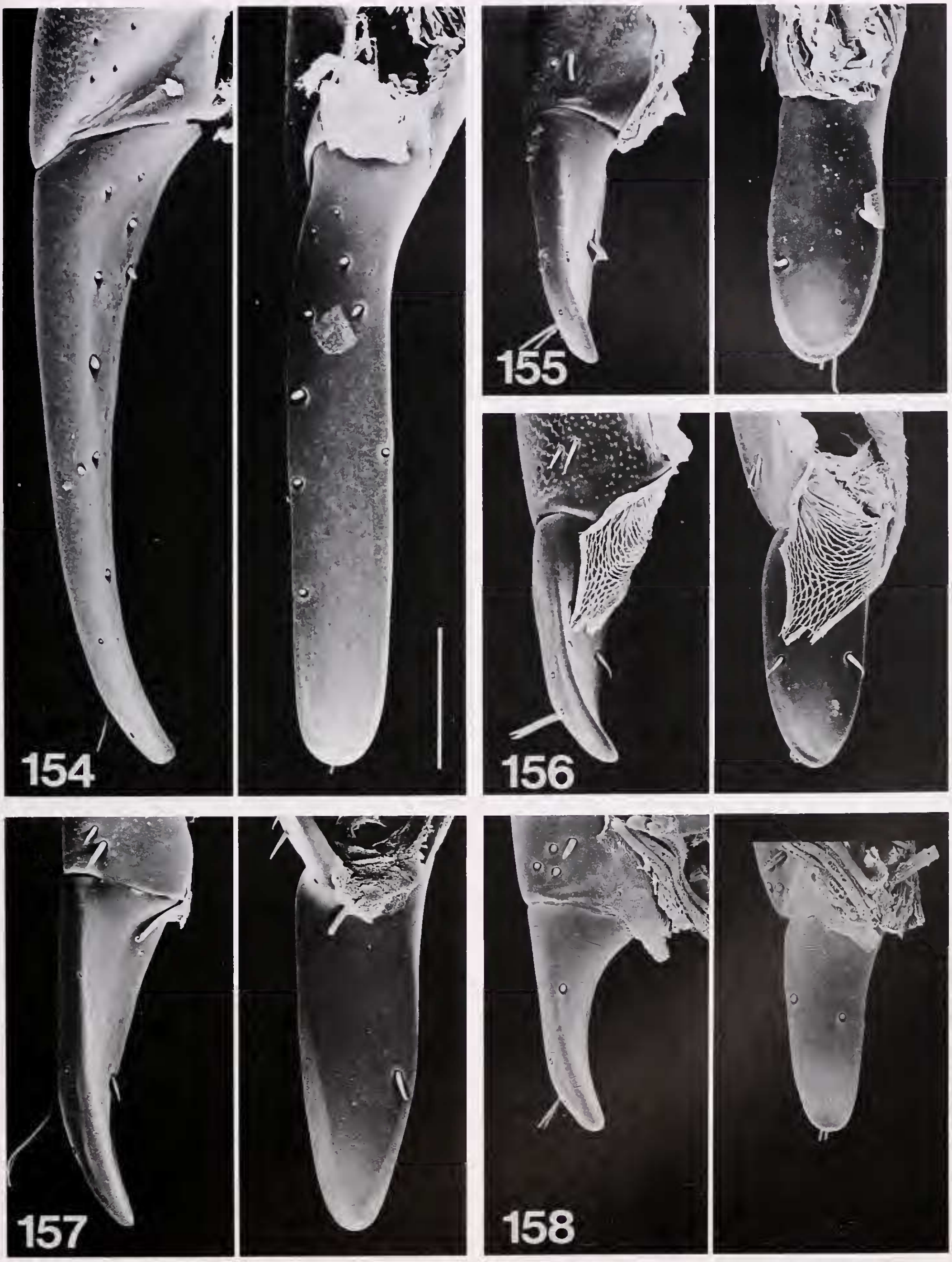
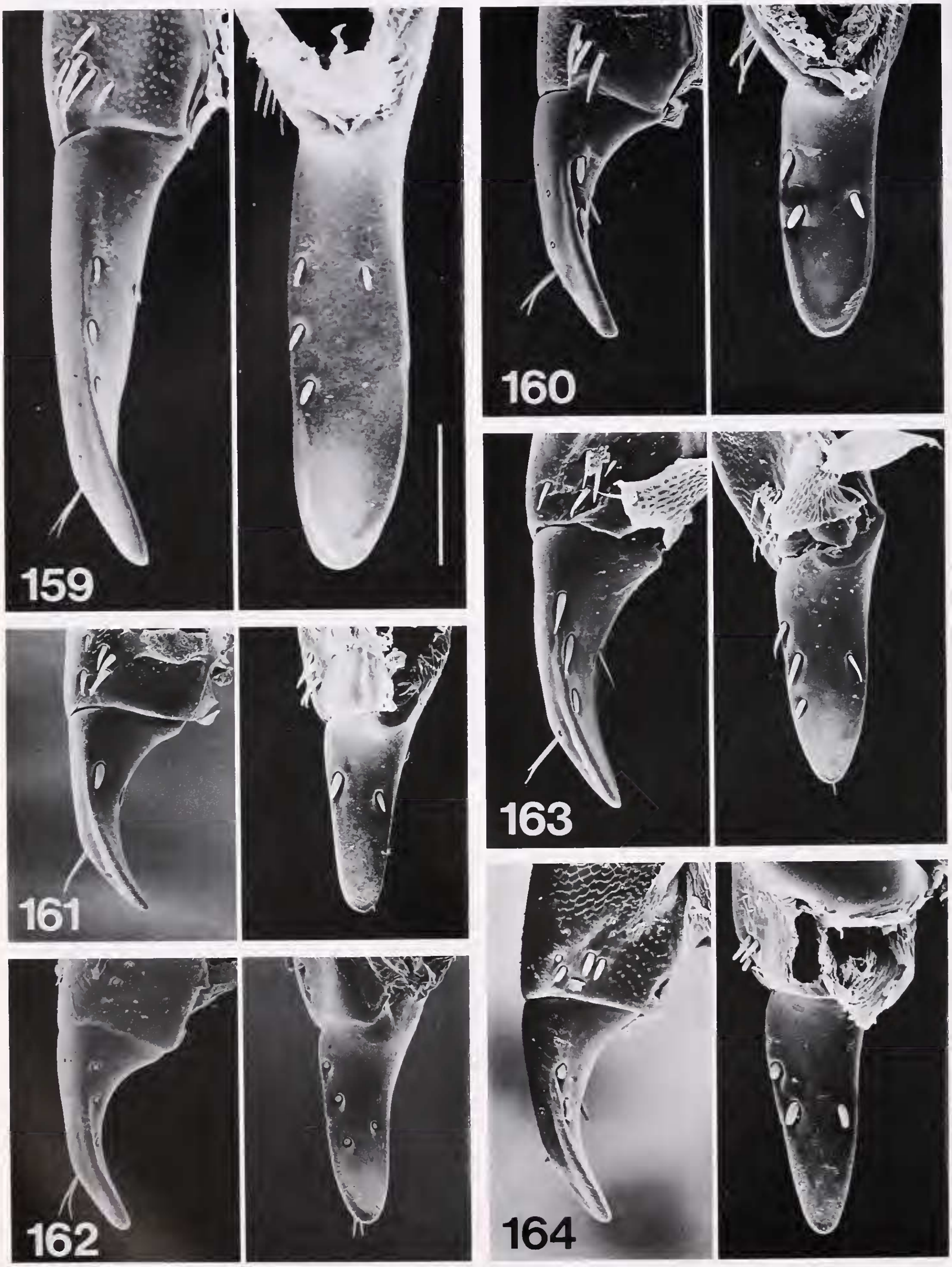
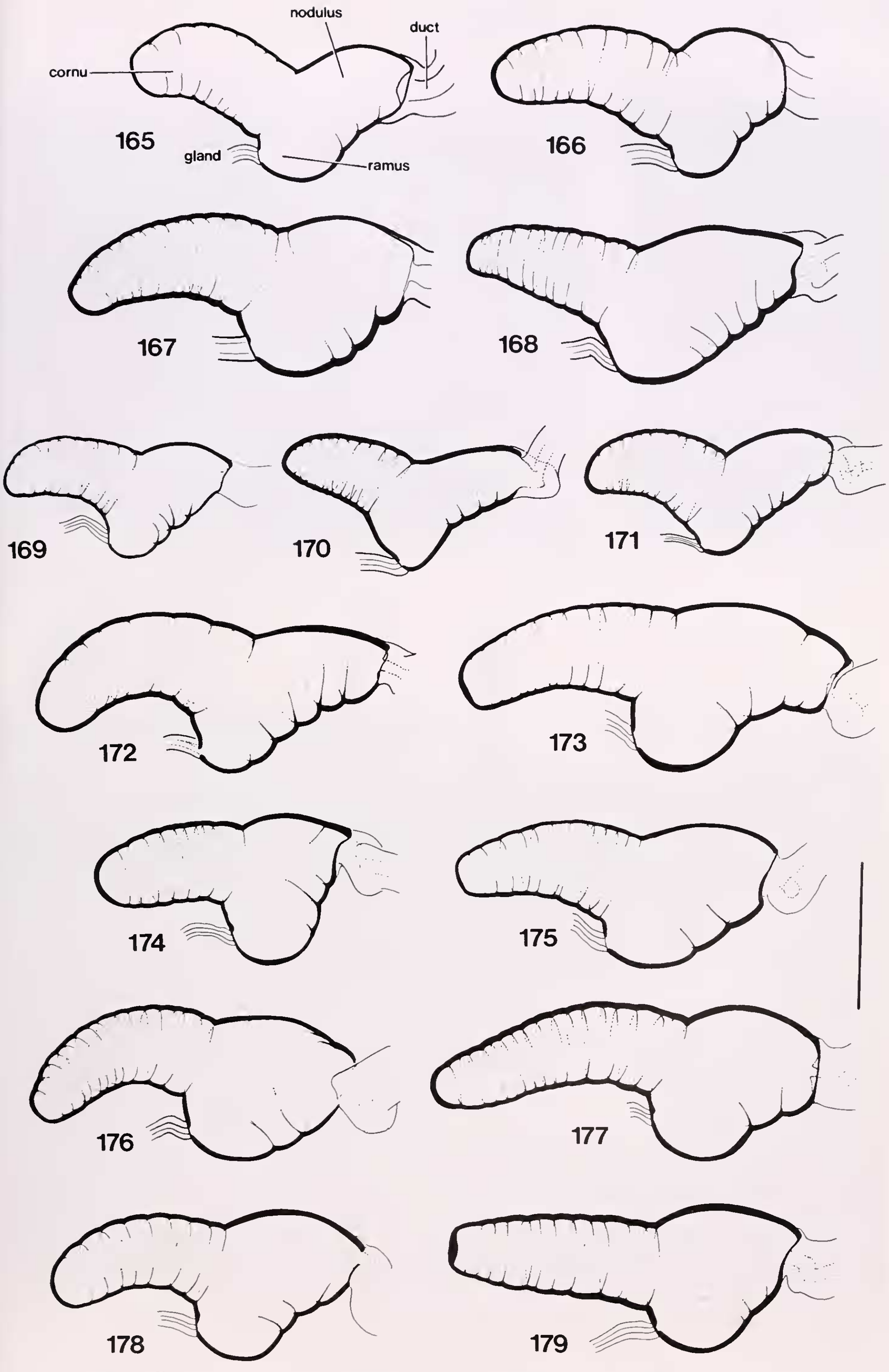
Figures 148–153. First and second left stylomeres of female genitalia. Scale bar = 100 μm; all figures at same scale. **Left-hand picture**: dorsal view. **Right-hand picture**: left lateral view. 148. *B. balli*. 149. *B. foveum*. 150. *B. argenteolum*. 151. *B. alaskense*. 152. *B. stenoderum*. 153. *B. punctatostriatum*.



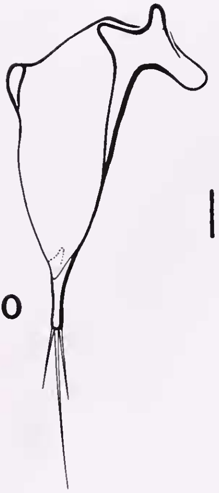
Figures 154–158. First and second left stylomeres of female genitalia. Scale bar = 100 μm; all figures at same scale. **Left-hand picture**: dorsal view. **Right-hand picture**: left lateral view. 154. *B. carinula.* 155. *B. velox.* 156. *B. lapponicum.* 157. *B. hesperium.* 158. *B. lorquinii.*



Figures 159–164. First and second left stylomeres of female genitalia. Scale bar = 100 μm; all figures at same scale. **Left-hand picture**: dorsal view. **Right-hand picture**: left lateral view. 159. *B. zephyrum;* specimen from northern Oregon. 160. *B. levettei levettei.* 161. *B. levettei carrianum.* 162. *B. inaequale.* 163. *B. litorale.* 164. *B. conicolle.*



Figures 165–179. Spermathecae of *Bracteon*. Scale bar = 100 μm; all figures at same scale. 165. *B. balli*. 166. *B. foveum*. 167. *B. argenteolum*. 168. *B. alaskense*. 169. *B. stenoderum*. 170. *B. carinula*. 171. *B. velox*. 172. *B. lapponicum*. 173. *B. punctatostriatum*. 174. *B. hesperium*. 175. *B. lorquinii*. 176. *B. zephyrum*. 177. *B. levettei carrianum*. 178. *B. inaequale*. 179. *B. litorale*.



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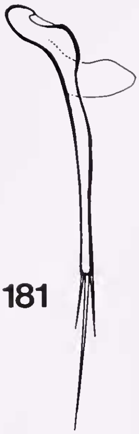

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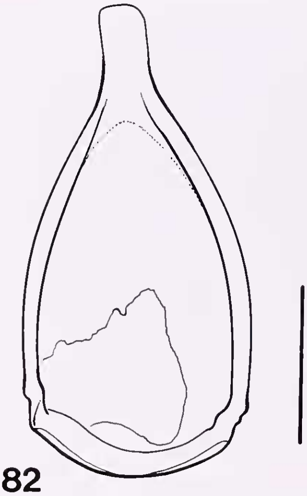

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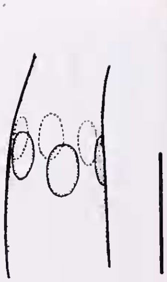

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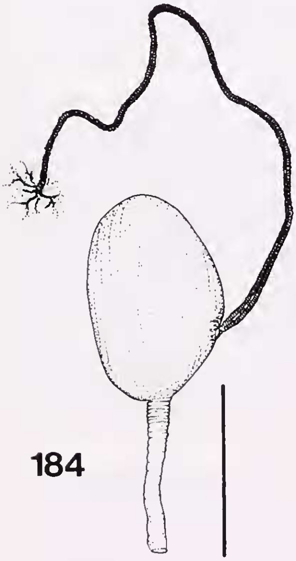

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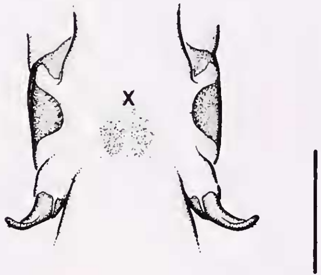

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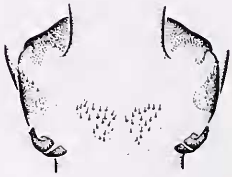

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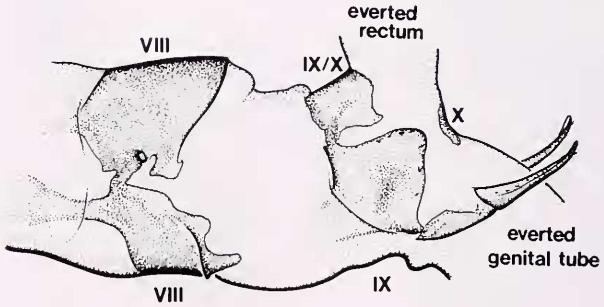


187

Figure 180. Left paramere of *B. levettei carrianum*. Right lateral view. Scale bar = 100 μm.

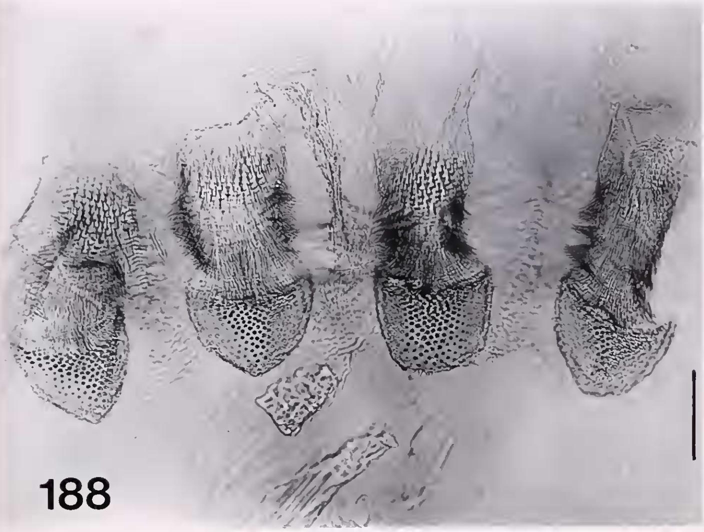
Figure 181. Right paramere of *B. levettei carrianum*. Left lateral view. Scale as previous figure.

Figure 182. Ring sclerite of *B. levettei carrianum*. Scale bar = 0.5 mm.

Figure 183. Rectal pads of *B. foveum*. Scale bar = 0.5 mm.

Figure 184. Cleared pygidial defense structures of *B. balli*. Left dorsal view. Scale bar = 0.5 mm.

Figures 185–187. Everted female genitalia. Scale bar = 0.5 mm. 185. Dorso-apical view of everted female genitalia of *B. carinula*. 186. Dorso-apical view of everted female genitalia of *B. balli*. 187. Left lateral view of everted female genitalia of *B. carinula*.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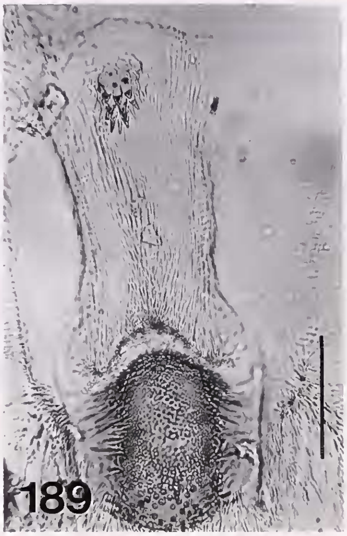
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Figures 188, 189. Proventriculi of *Bembidion*. Scale bars = 100 μm. 188. *B. carinula*. 189. *B. (Ocys) harpaloides*. Only one of four lobes shown.

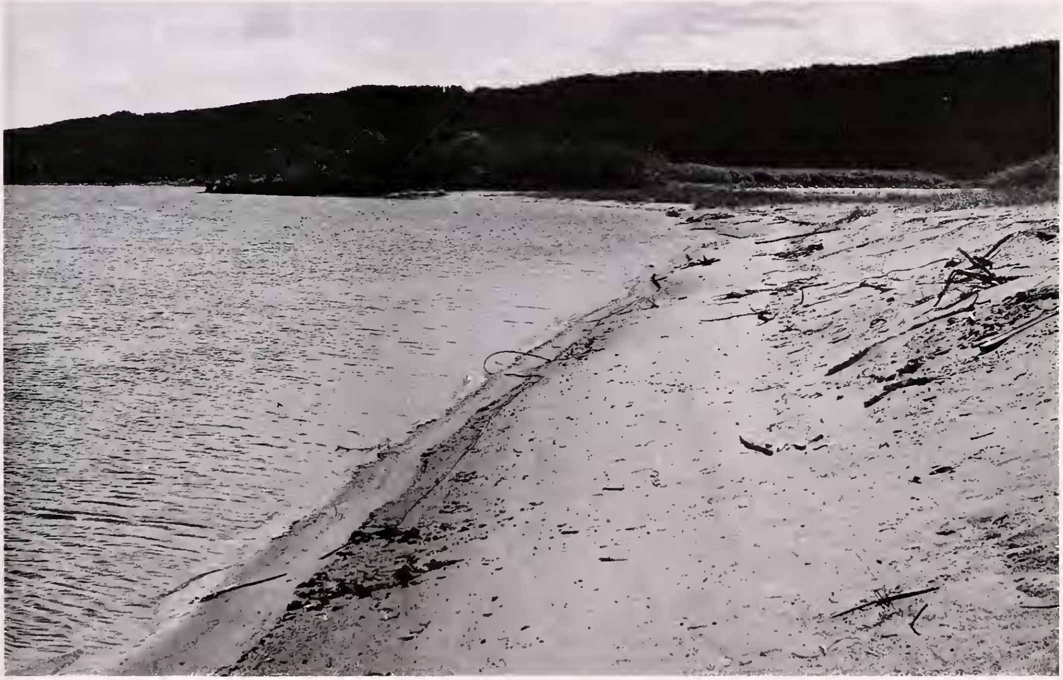


Figure 190. North Saskatchewan River bank at Paynton Ferry, Saskatchewan. Habitat of *B. balli*, *B. foveum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, and *B. levettei carrianum*, as well as the related *B. coxendix* and *B. bifossulatum cheyennense*.

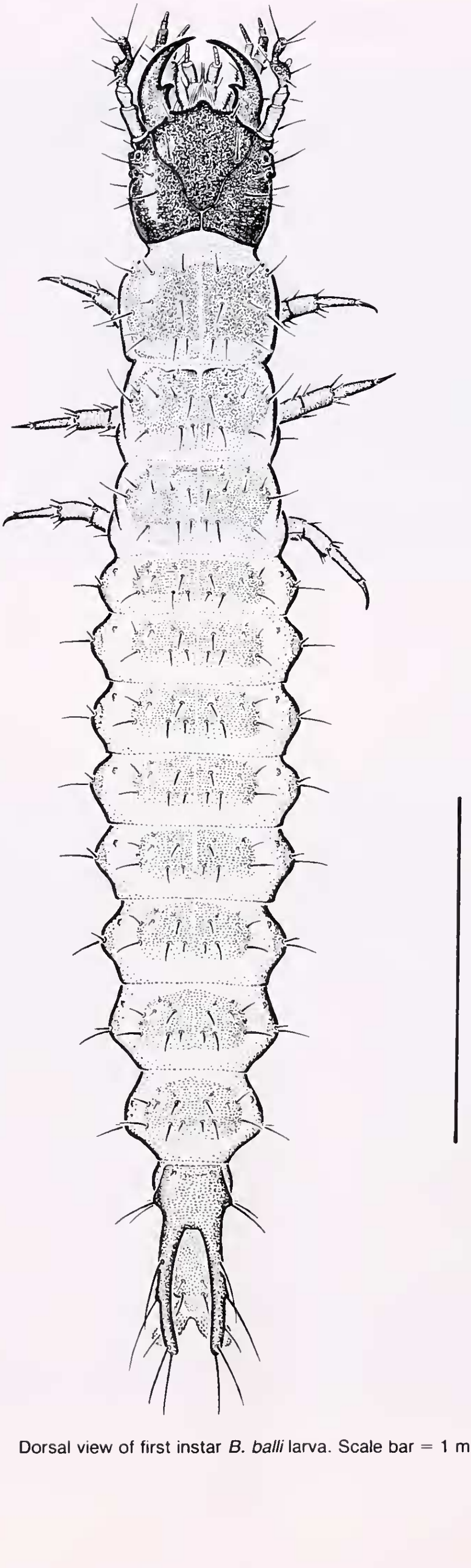
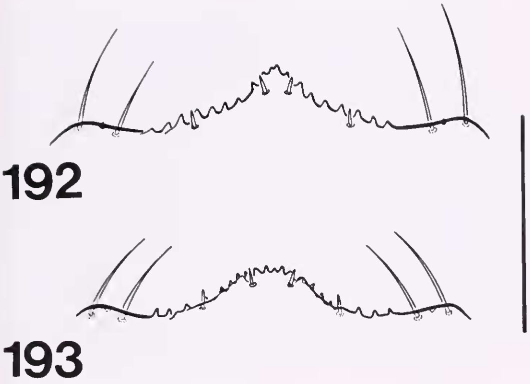


Figure 191. Dorsal view of first instar *B. balli* larva. Scale bar = 1 mm.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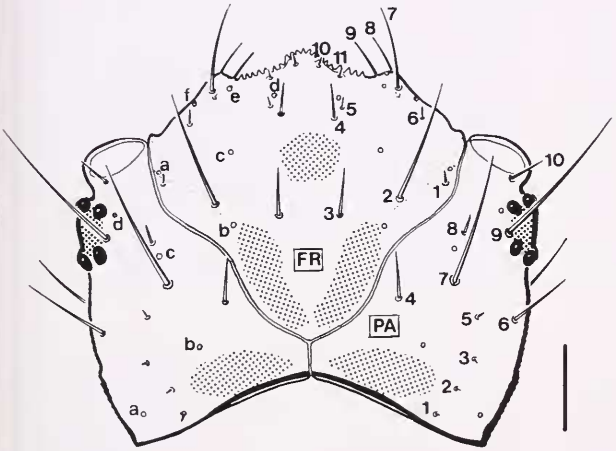

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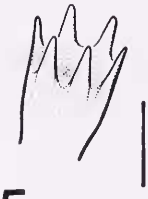
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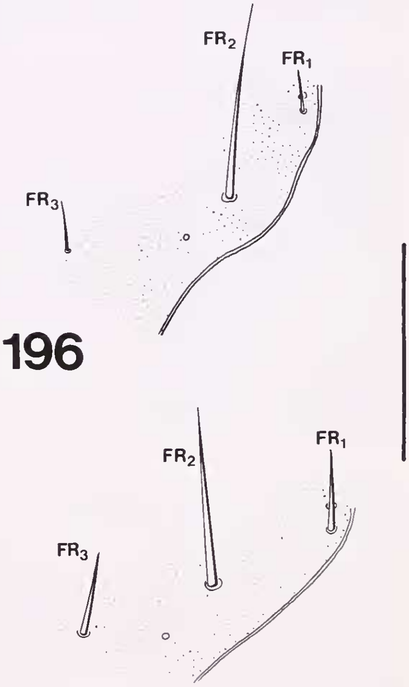

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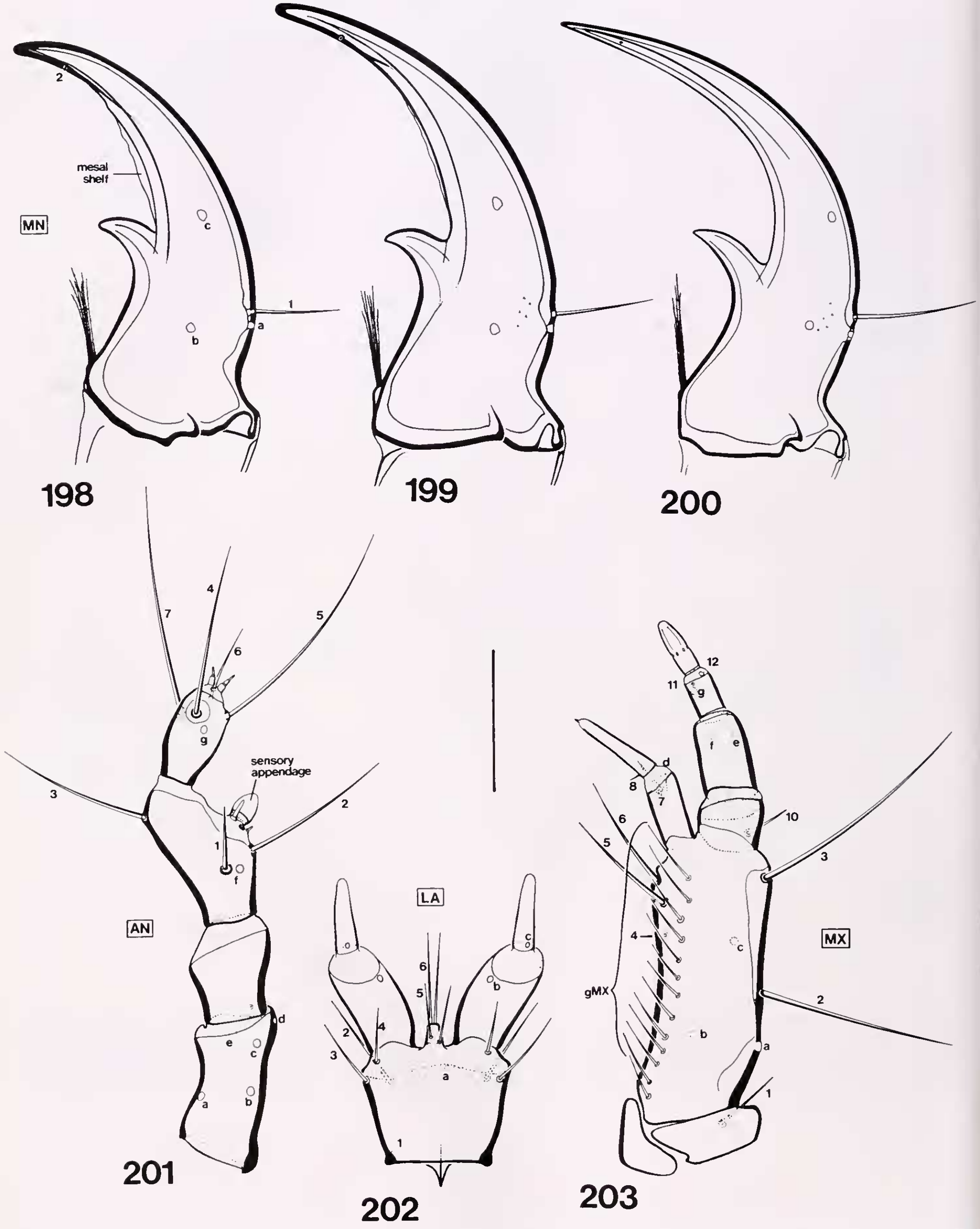
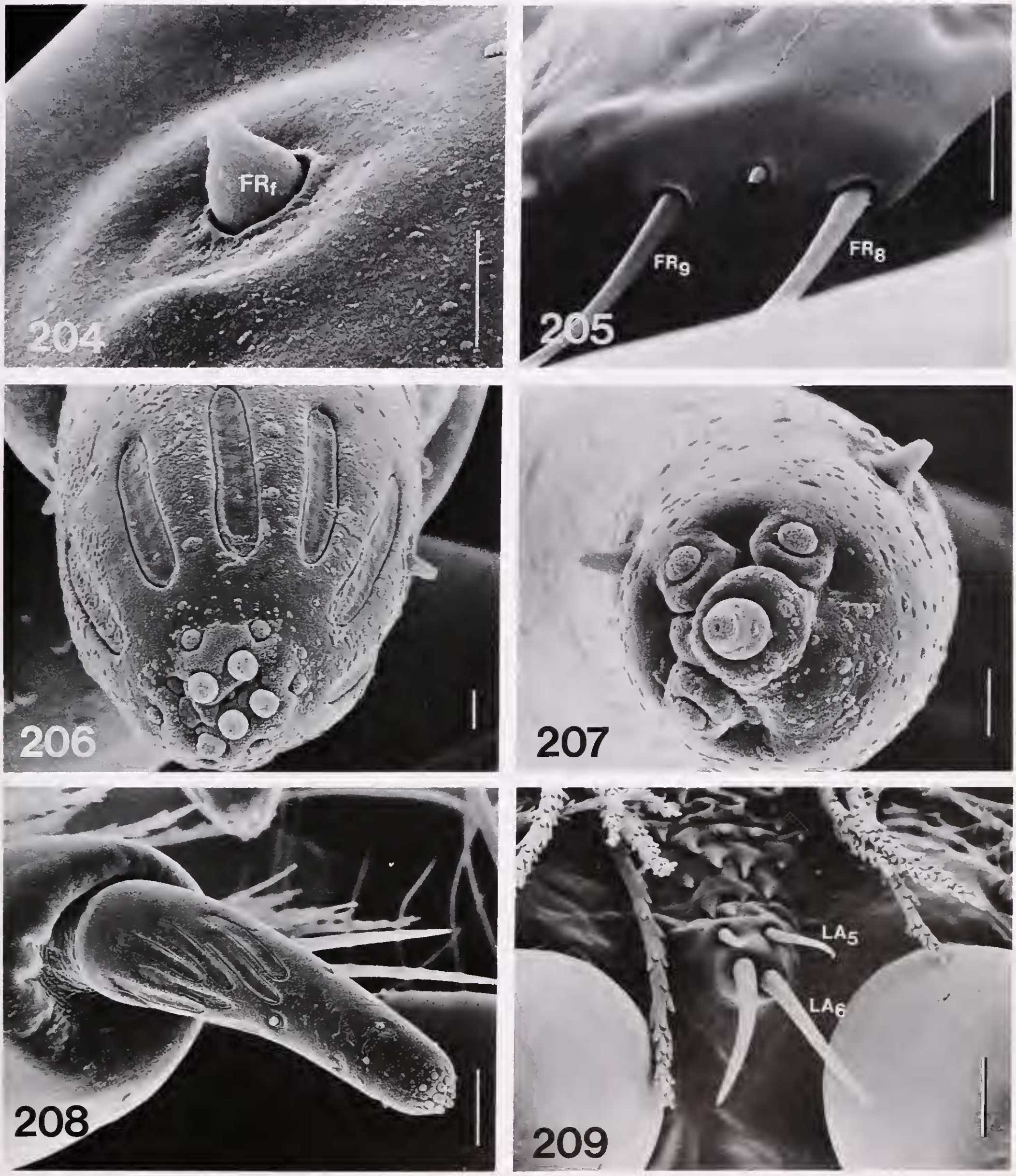
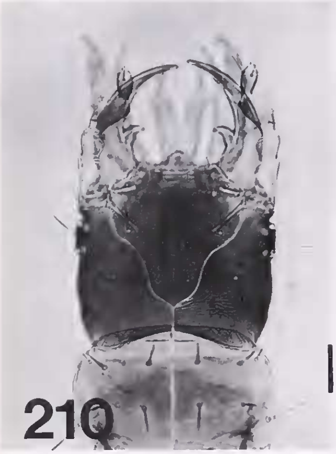
Figures 192–197. Bembidiine larvae. Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature (Bousquet and Goulet, 1984). Scale bars all 100 μm, except for Figure 195, for which scale bar = 10 μm. Figure 192 at same scale as Figure 193. Figure 196 at same scale as Figure 197. 192. Nasale of first instar *B. coxendix*. 193. Nasale of first instar *B. inaequale*. 194. Head of first instar *B. punctatostriatum*, dorsal view. 195. Apex of seta FR_2 of first instar *Asaphidion alaskanum*. 196. Right central portion of frontale of first instar *B. balli*. 197. Right central portion of frontale of first instar *B. carinula*.



Figures 198–203. Cleared head structures of larval *Bembidion*. Scale bar = 100 μm. Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. 198. Right mandible of first instar *B. carinula*, dorsal view. Note wide mesal shelf. 199. Right mandible of first instar *B. foveum*, dorsal view. Note narrow mesal shelf. 200. Right mandible of first instar *B.* (*Odontium*) *coxendix*, dorsal view. 201. Right antenna of first instar *B. foveum*, dorsal view. 202. Labium of first instar *B. foveum*, dorsal view. 203. Right maxilla of first instar *B. foveum*, dorsal view.



Figures 204–209. Structures of larval *Bracteon*. 204. Sensillum FR_f in first instar *B. punctatostriatum*. Scale bar = 2 μm. 205. Small sensillum between FR_8 and FR_9 in first instar *B. foveum*. Scale bar = 10 μm. 206. Apex of maxillary palpus of first instar *B. lapponicum*. Scale bar = 2 μm. 207. Apex of galea of first instar *B. lapponicum*. Scale bar = 2 μm. 208. Apical article of labial palpus of first instar *B. lapponicum*. Scale bar = 10 μm. 209. Anterior view of ligular region of *B. lapponicum*. Note quadrisetose ligula and multiply branched setae. Scale bar = 20 μm.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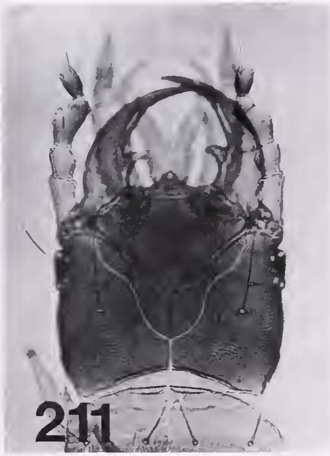
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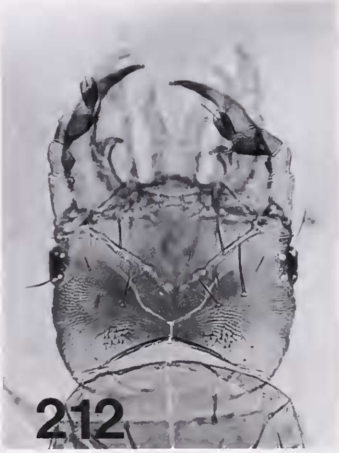
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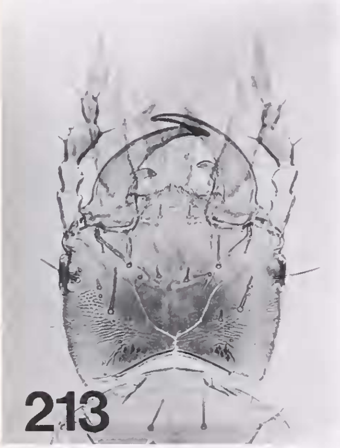
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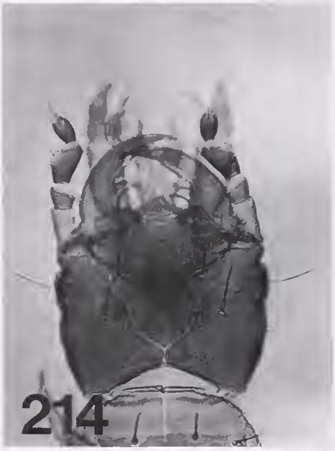
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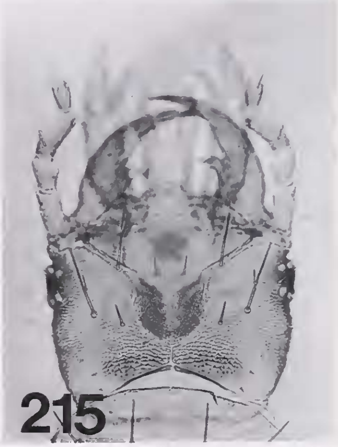
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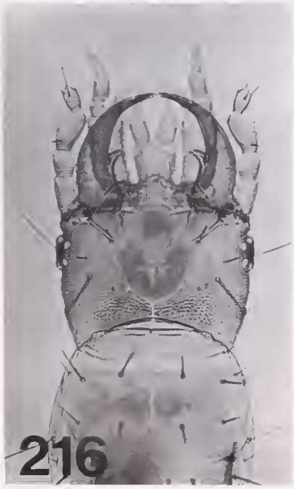
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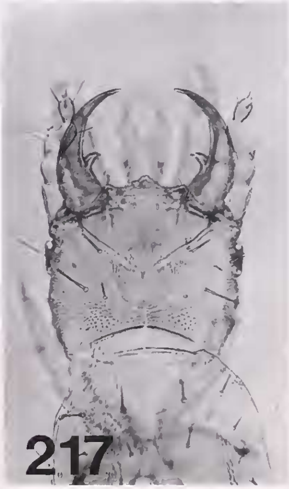
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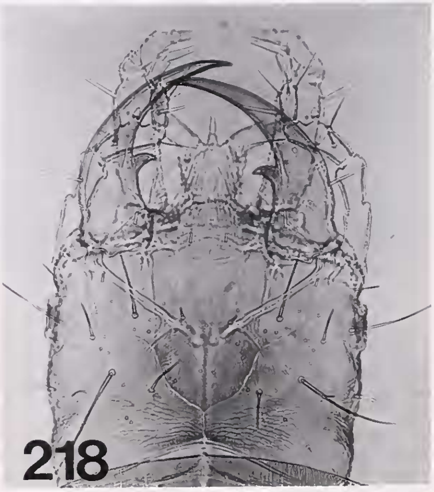
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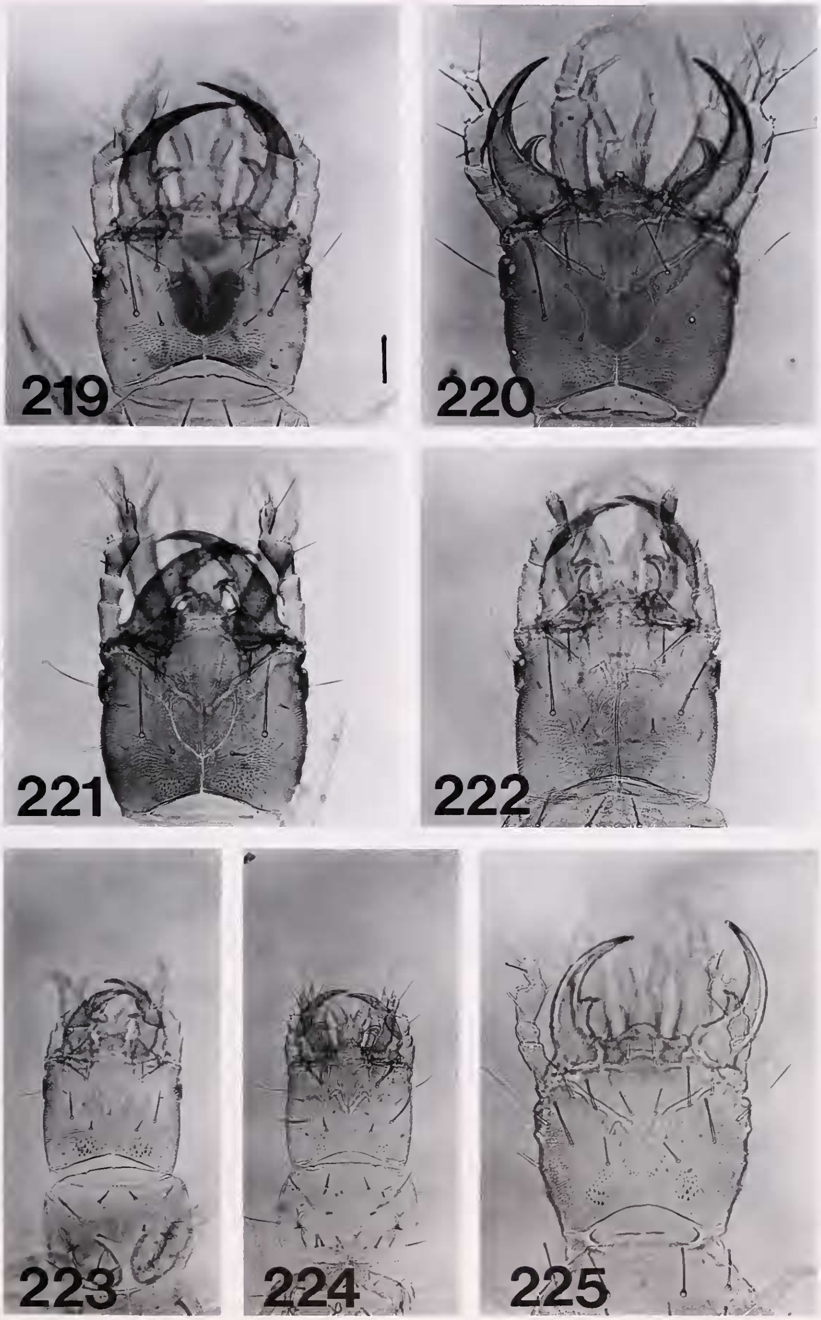
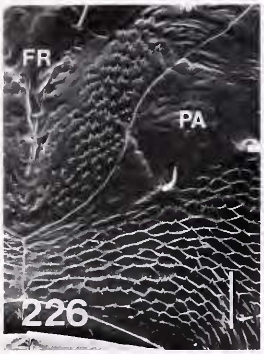
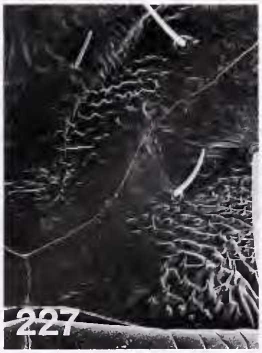
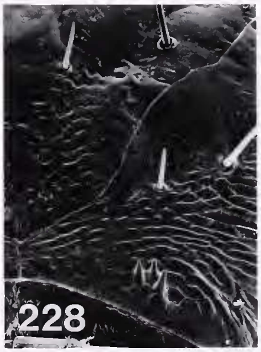
Figures 210–217. Cleared heads of first instar larvae. Scale bar = 100 μm; all figures at same scale. 210. *B. balli.* 211. *B. foveum.* 212. *B. alaskense.* 213. *B. carinula.* 214. *B. lapponicum.* 215. *B. punctatostriatum.* 216. *B. lorquinii.* 217. *B. zephyrum.* Figure 218. Cleared head of second instar *B. levettei levettei* larva. Same scale as Figures 210–217.

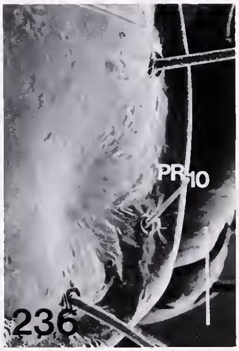


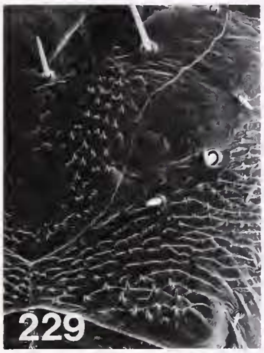
Figures 219–225. Cleared heads of first instar larvae. Scale bar = 100 μm; all figures at same scale. 219. *B. coxendix*. 220. *B. bifossulatum cheyennense*. 221. *B. chalceum*. 222. *B. antiquum*. 223. *B. aenulum*. 224. *B. obtusum*. 225. *Asaphidion alaskanum*.

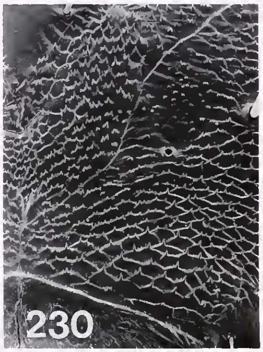


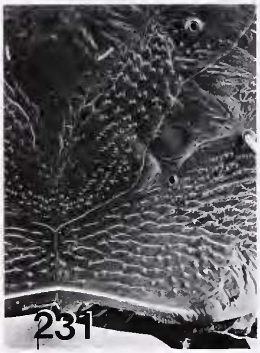


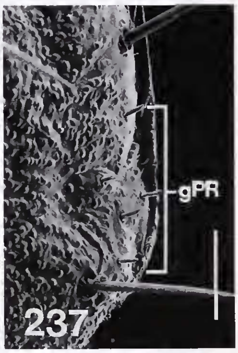


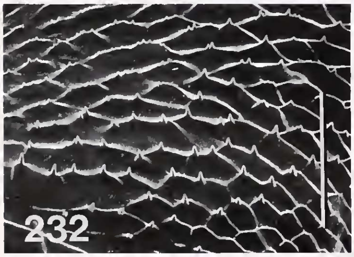


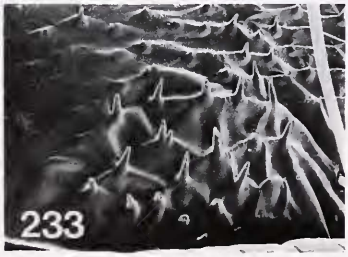


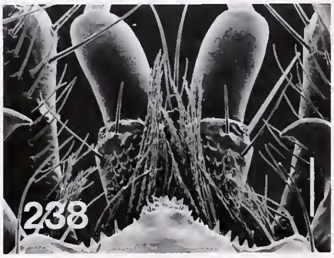


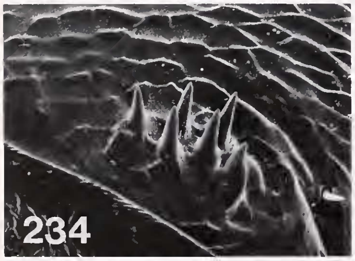


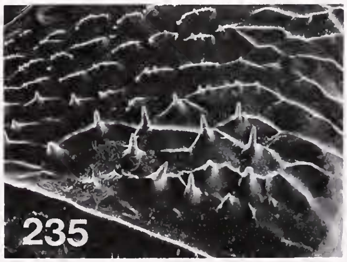


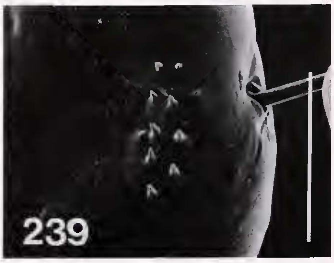








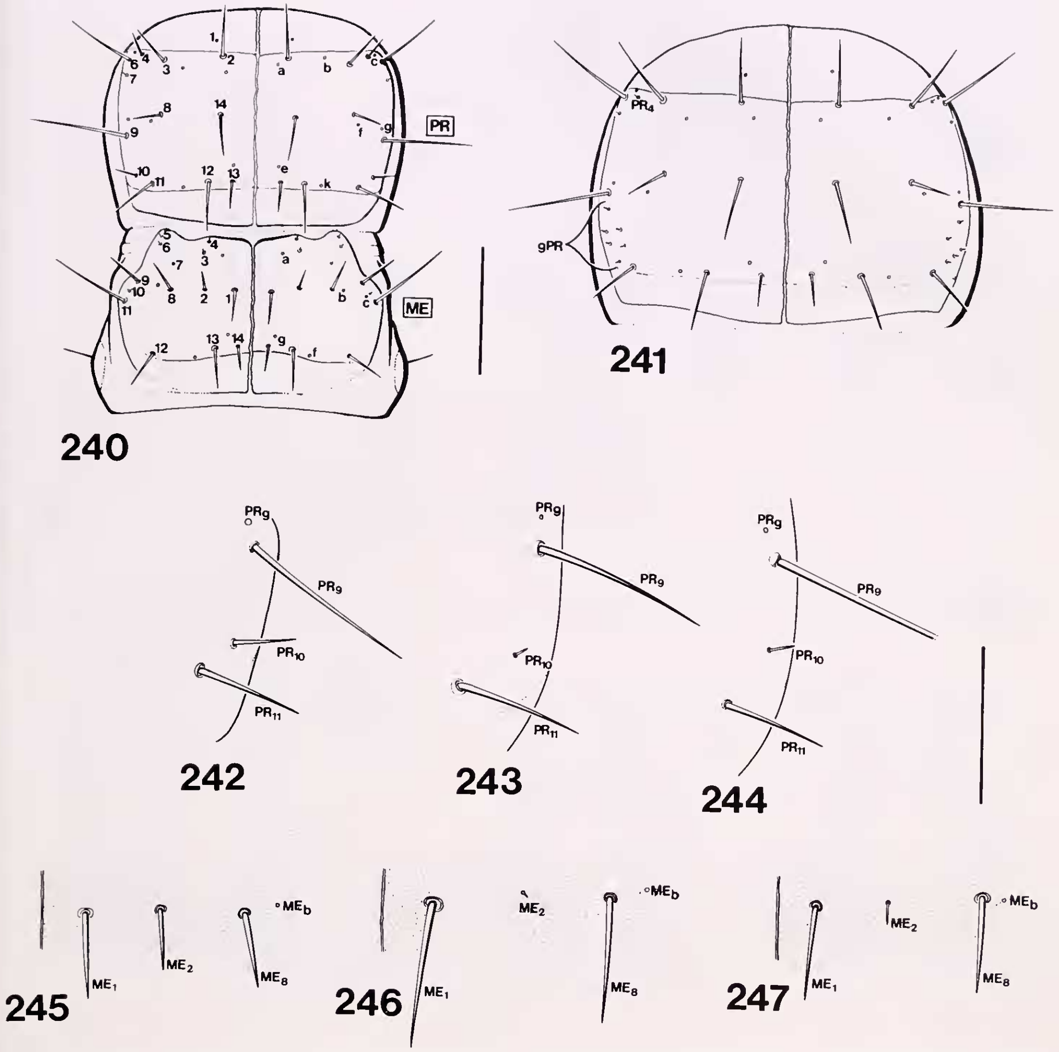




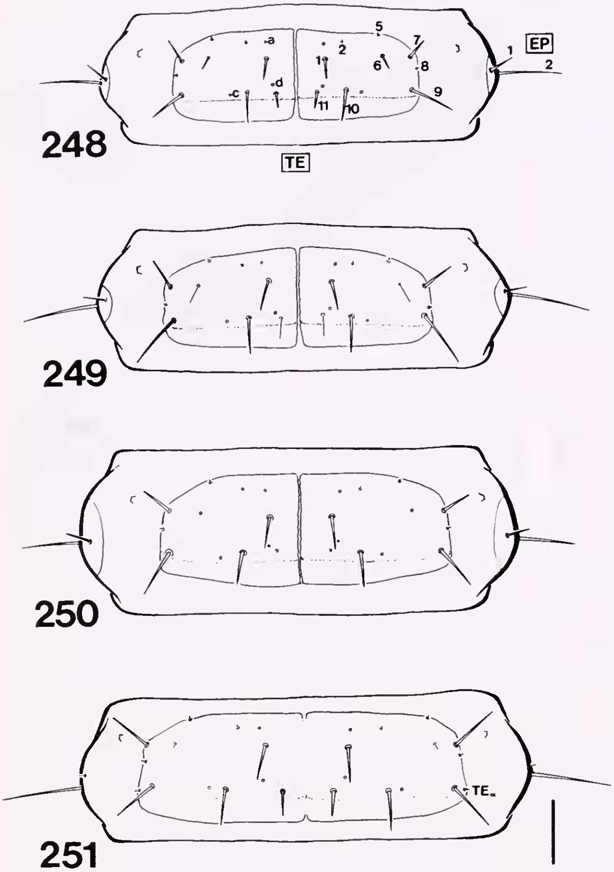
Figures 226–231. First instar *Bracteon*, central and right portions of posterior part of head. Scale bar = 40 μm. 226. *B. foveum*. 227. *B. alaskense*. 228. *B. carinula*. 229. *B. lapponicum*. 230. *B. punctatostriatum*. 231. *B. levettei levettei*.

Figures 232–235. Parietal egg bursters. Scale bar = 40 μm. 232. *B. foveum*. 233. *B. alaskense*. 234. *B. carinula*. 235. *B. lapponicum*.

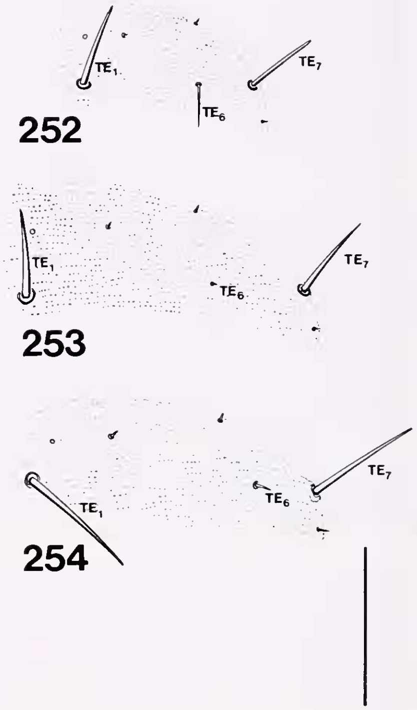
Figures 236–239. First instar *Bracteon*. Scale bars = 40 μm. 236. Right basal corner of pronotum of *B. alaskense*. 237. Right basal corner of pronotum of *B. punctatostriatum*. 238. Dorsal view of nasale and mouth cavity of *B. foveum*. 239. Dorsal view of right mandible of *B. punctatostriatum* near seta MN_1.



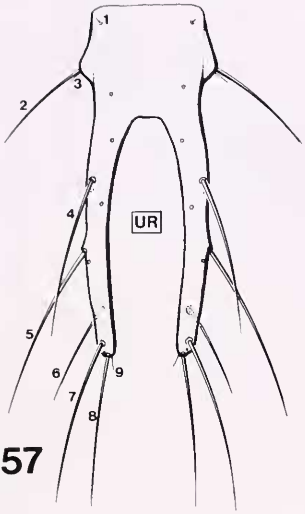
Figures 240–247. Thoraces of larval *Bembidion.* Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. Figure 240 at same scale as Figure 241; scale bar = 200 μm. Figures 242–247 at same scale; scale bar = 100 μm. 240. Pronotum and mesonotum of first instar *B. balli.* 241. Pronotum of first instar *B. punctatostriatum.* 242. Right basilateral corner of pronotum of first instar *B. balli.* 243. Right basilateral corner of pronotum of first instar *B. carinula.* 244. Right basilateral corner of pronotum of first instar *B. integrum.* 245. Right-central portion of mesonotum of first instar *B. balli.* 246. Right-central portion of mesonotum of first instar *B. carinula.* 247. Right-central portion of mesonotum of first instar *B. antiquum.*



Figures 248–251. Second abdominal terga of first instar *Bracteon.* Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. All at same scale; scale bar = 100 μm. 248. *B. balli.* 249. *B. foveum.* 250. *B. carinula.* 251. *B. punctatostriatum.*



Figures 252–254. Right anterior portion of second abdominal terga of first instar *Bracteon,* showing variation in sizes of seta TE$_6$. All at same scale; scale bar = 100 μm. 252. *B. balli.* 253. *B. carinula.* 254. *B. punctatostriatum.*



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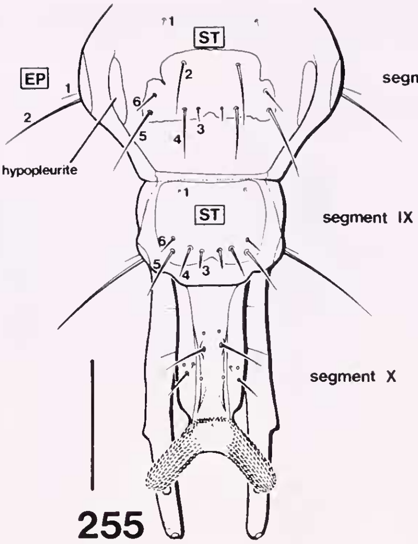

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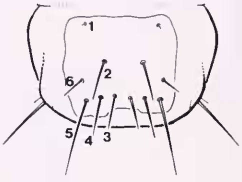

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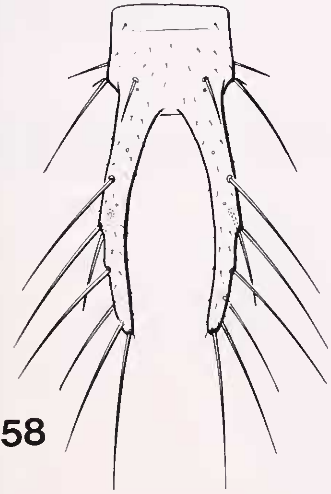

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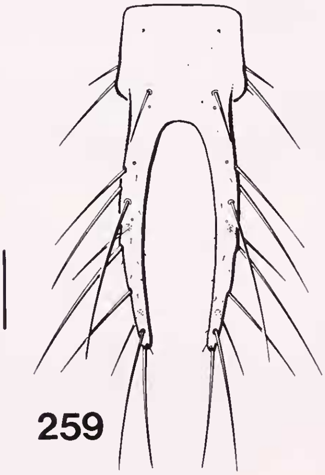

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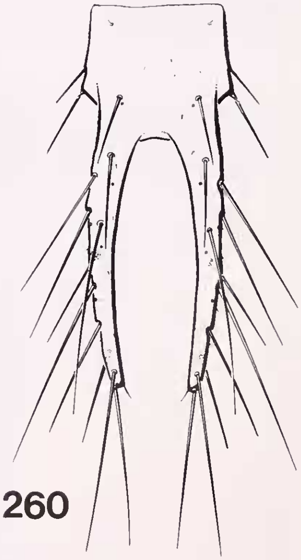


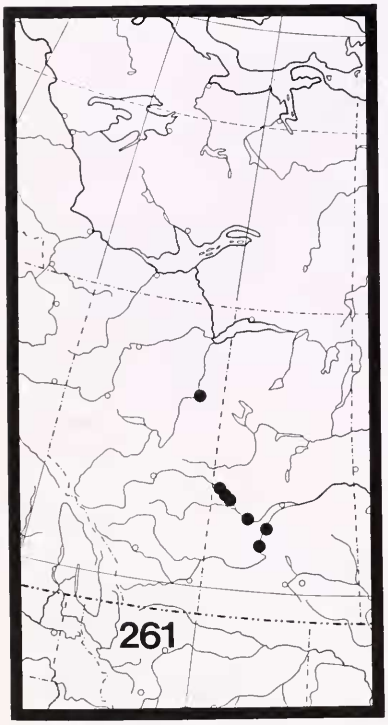
260

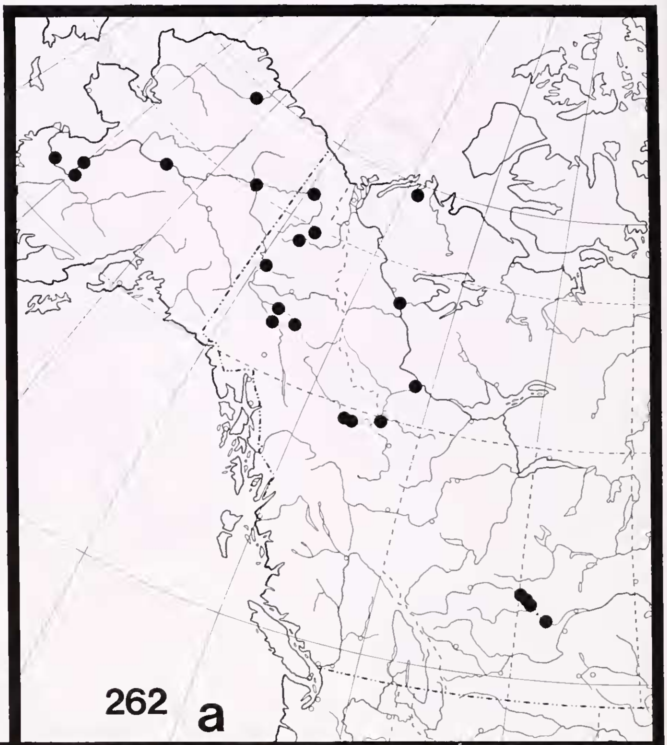
Figure 255. Ventral view of abdominal segments VIII through X of first instar *B. balli.* Scale bar = 200 μm.

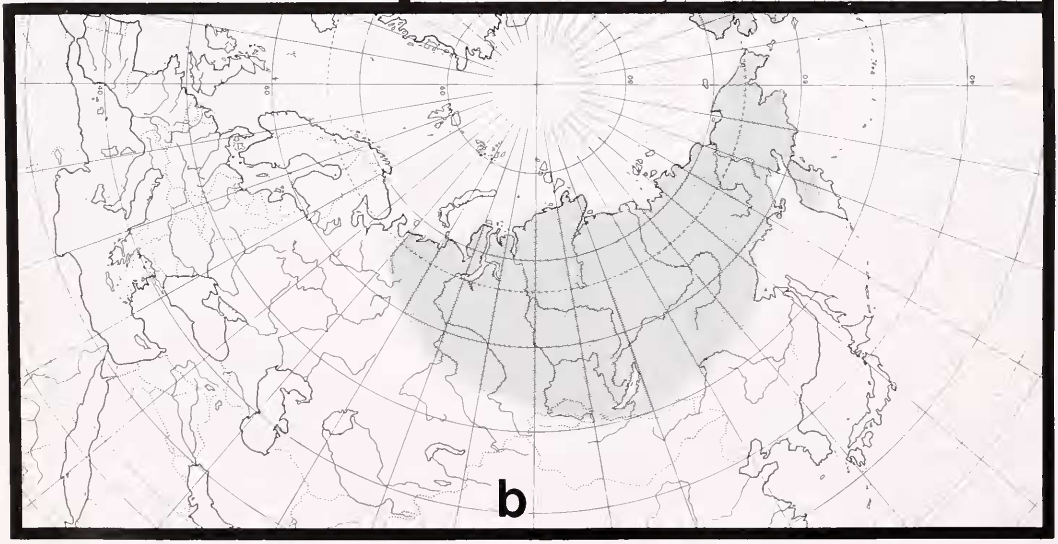
Figure 256. Ventral view of abdominal segment IX of first instar *B. carinula.* Same scale as Figure 255.

Figures 257. Urogomphi of first instar *B. balli*, dorsal view. Same scale as Figure 255.

Figures 258–260. Urogomphi of second instar *Bracteon*, dorsal view. Figures 258–260 at same scale; scale bar = 200 μm. 258. *B. balli.* 259. *B. lapponicum.* 260. *B. carinula.*

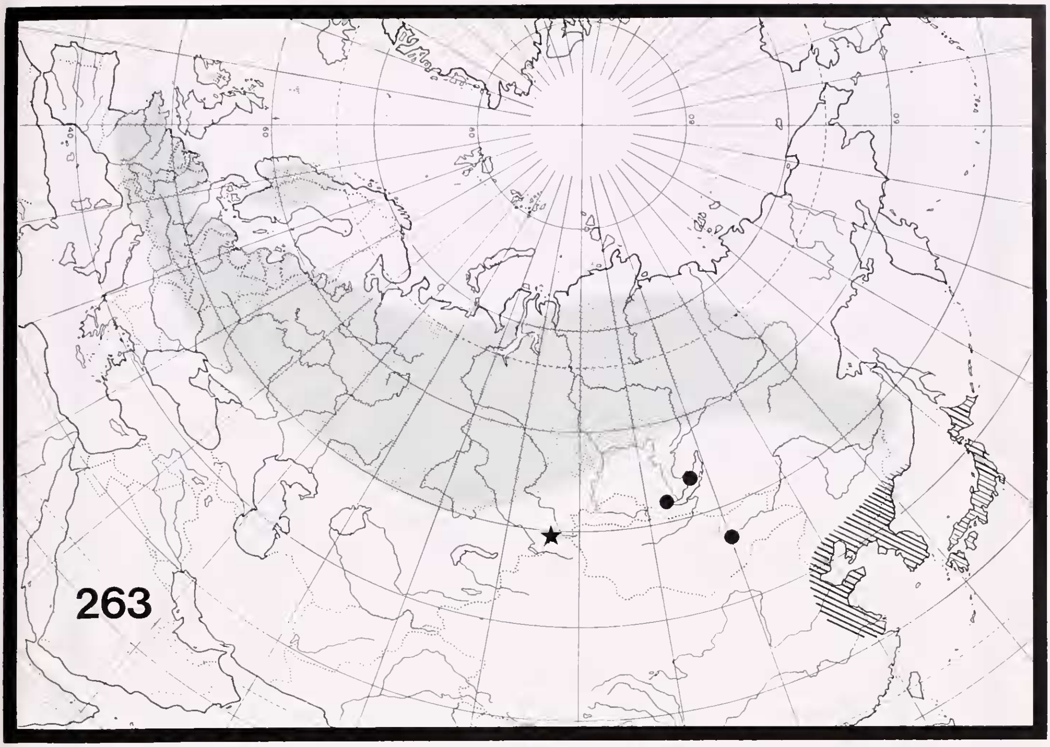






Figures 261, 262. Geographic distributions of species of *Bracteon*. 261. *B. balli*. 262. *B. foveum*. **a.** Nearctic distribution. It is also known from Churchill, Manitoba, off the eastern edge of the map. **b.** Approximate Palearctic distribution. Based on Lindroth (1962) and personal observations.

263



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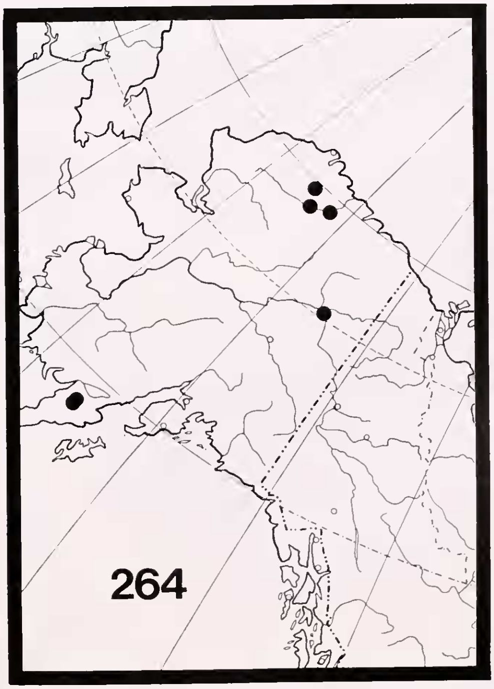
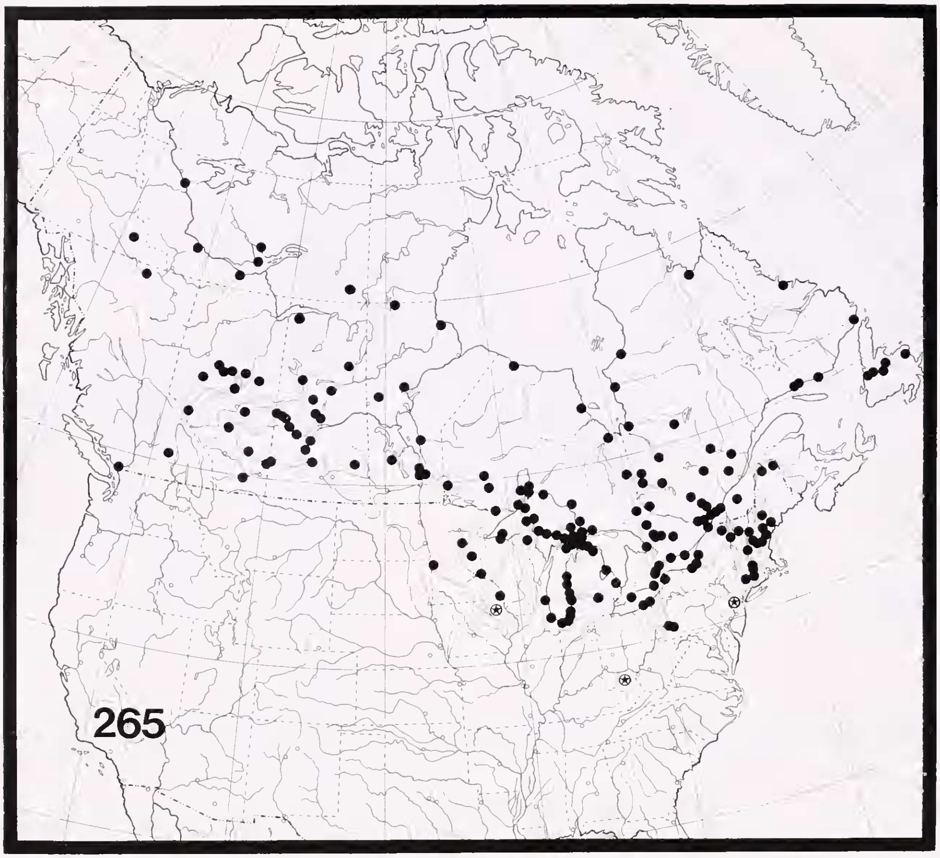


Figures 263, 264. Geographic distributions of species of *Bracteon*. 263. *B. argenteolum* (stippled), Palearctic *B. alaskense* (dots), *B. semenovi* (star), and *B. stenoderum* (striped). Approximate distributions of *B. argenteolum* and *B. stenoderum* based on Lindroth (1962), Netolitzky and Meyer (1933), Turin *et al.* (1977), and personal observations. 264. Nearctic distribution of *B. alaskense*.



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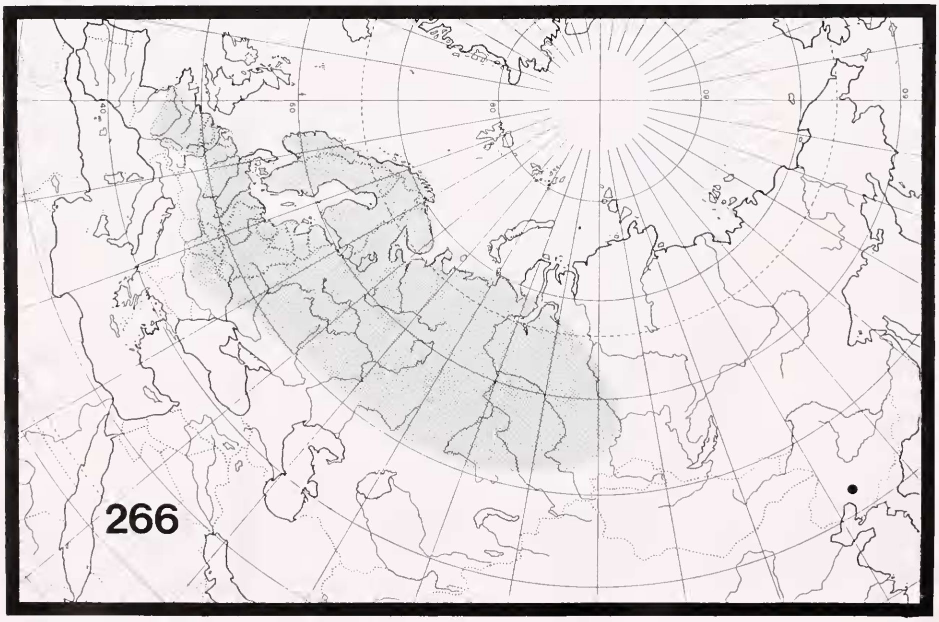


266

Figures 265, 266. Geographic distributions of species of *Bracteon*. 265. *B. carinula;* circled stars represent state records. 266. *B. velox*. Based on Lindroth (1962), Netolitzky and Meyer (1939), Turin *et al.* (1977), Kirschenhofer (1984), and personal observations.

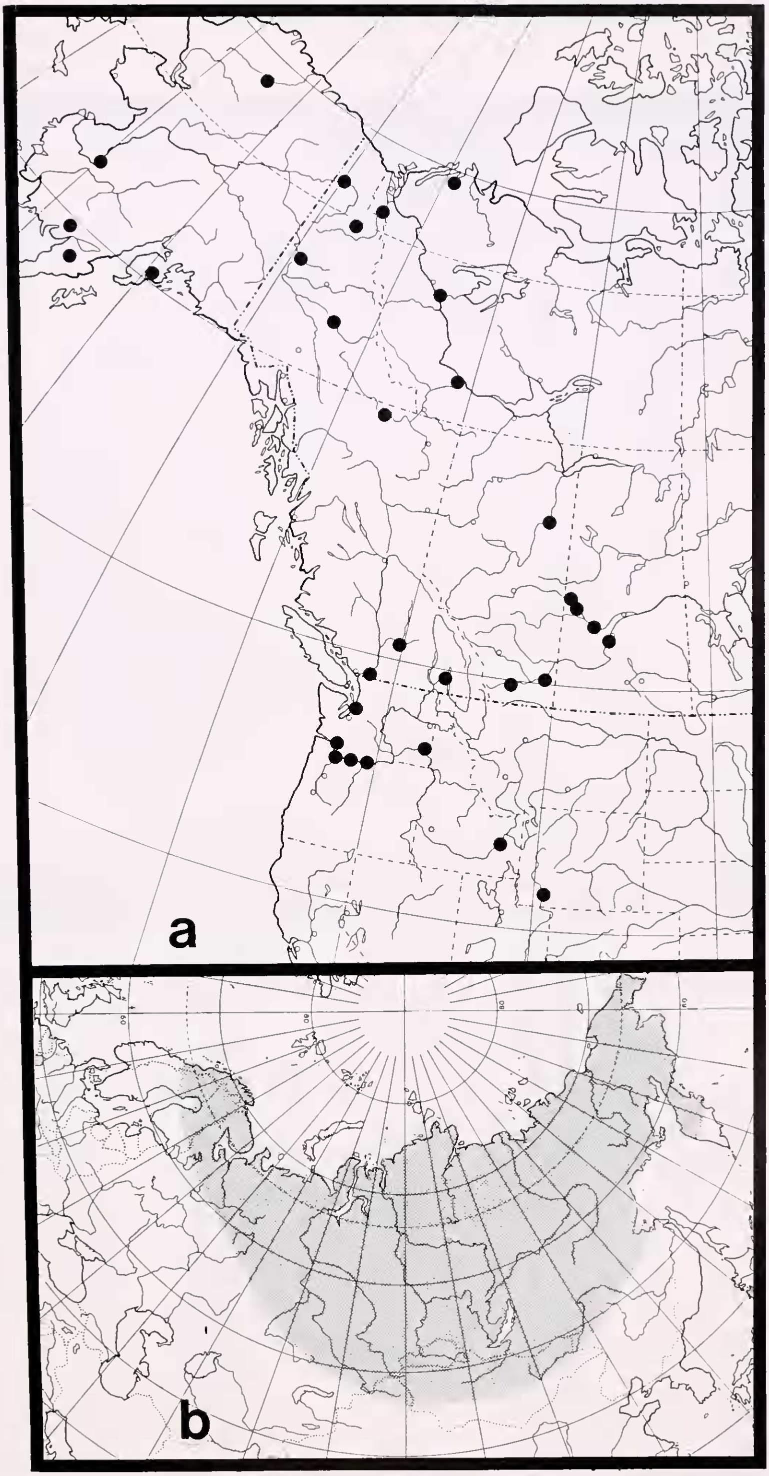
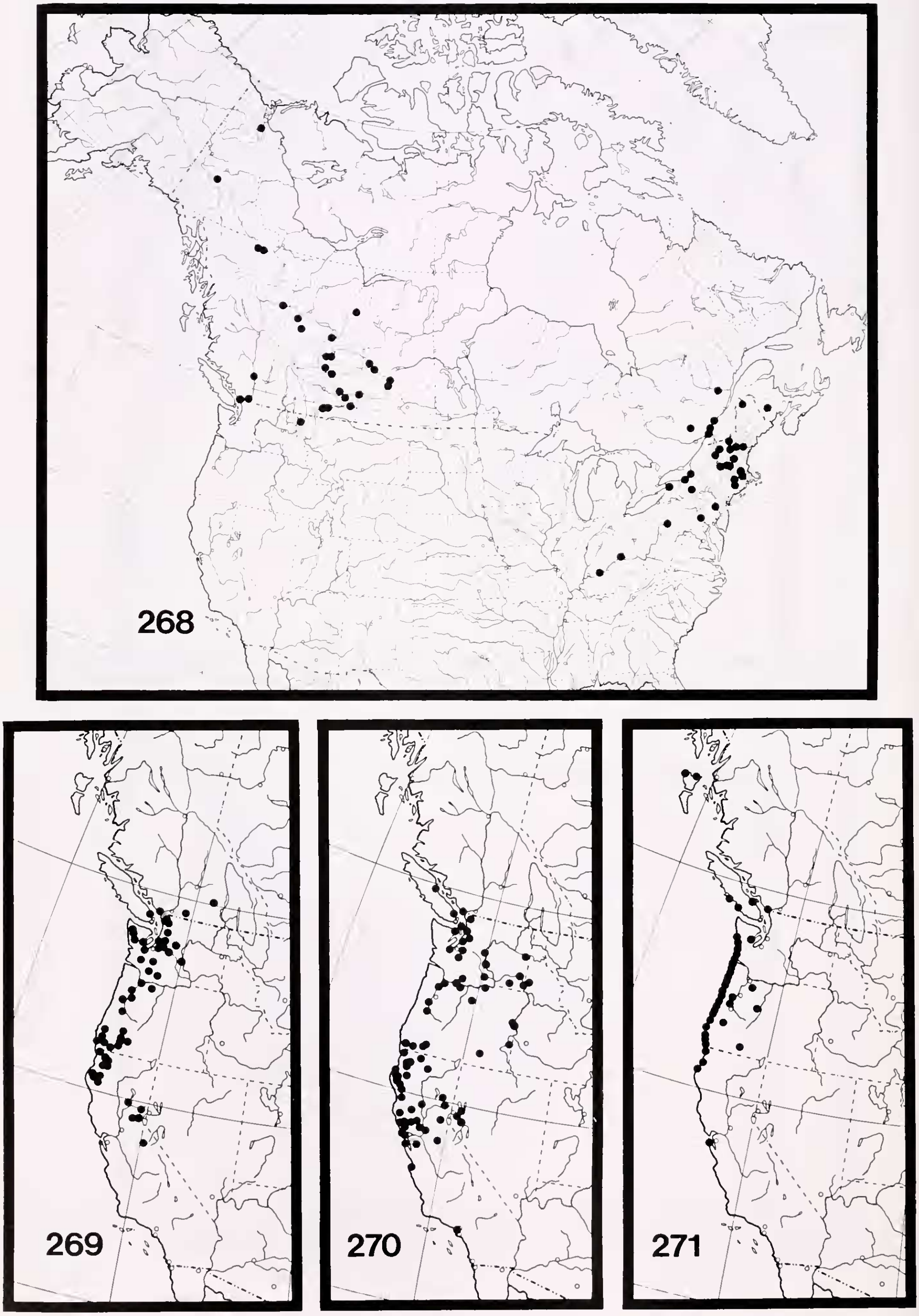


Figure 267. Geographic distribution of *B. lapponicum*. **a.** Nearctic distribution. **b.** Approximate Palearctic distribution. Based on Lindroth (1962) and personal observations.



Figures 268–271. Geographic distributions of species of *Bracteon*. 268. *B. punctatostriatum*. 269. *B. hesperium*. 270. *B. lorquinii*. 271. *B. zephyrum*.

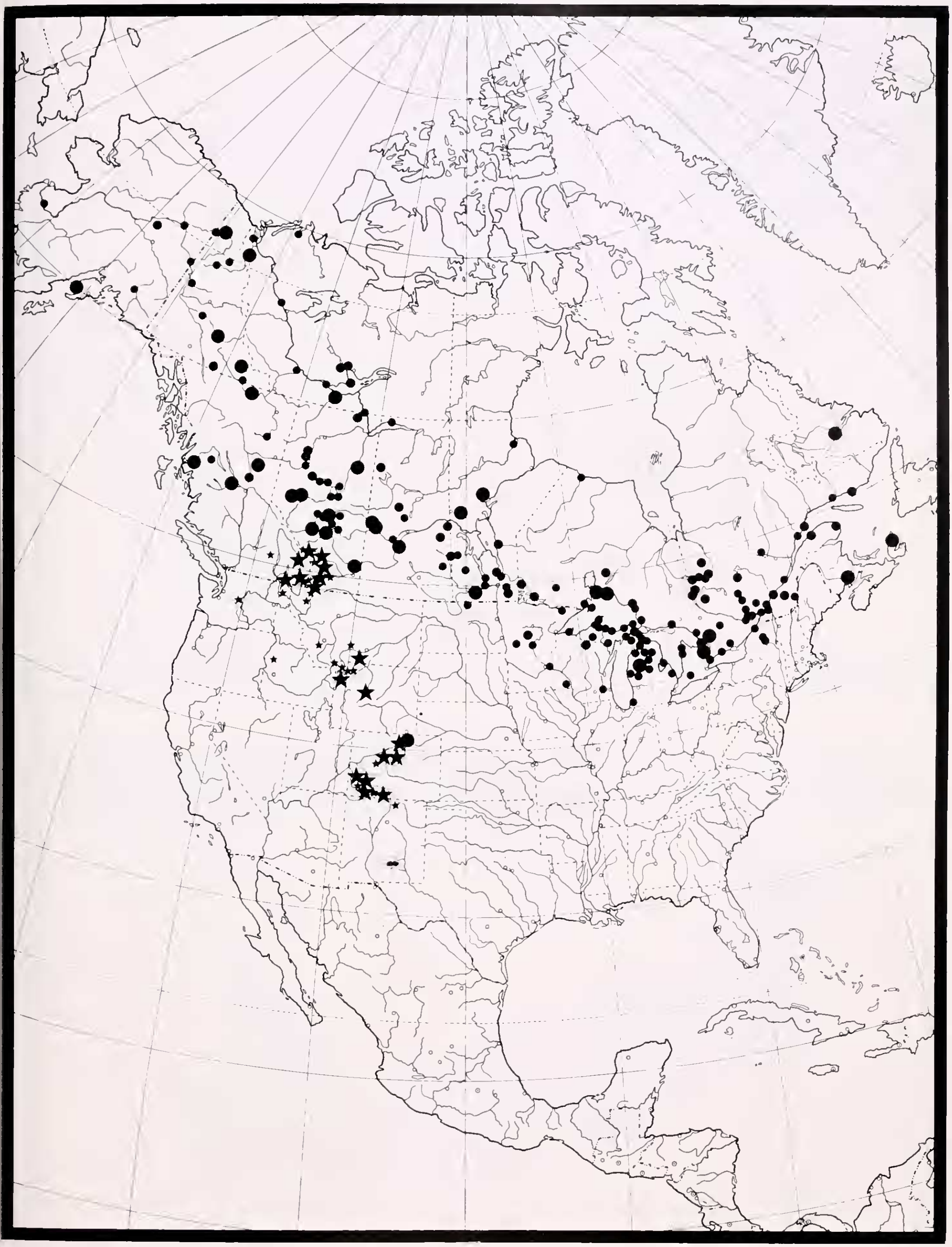
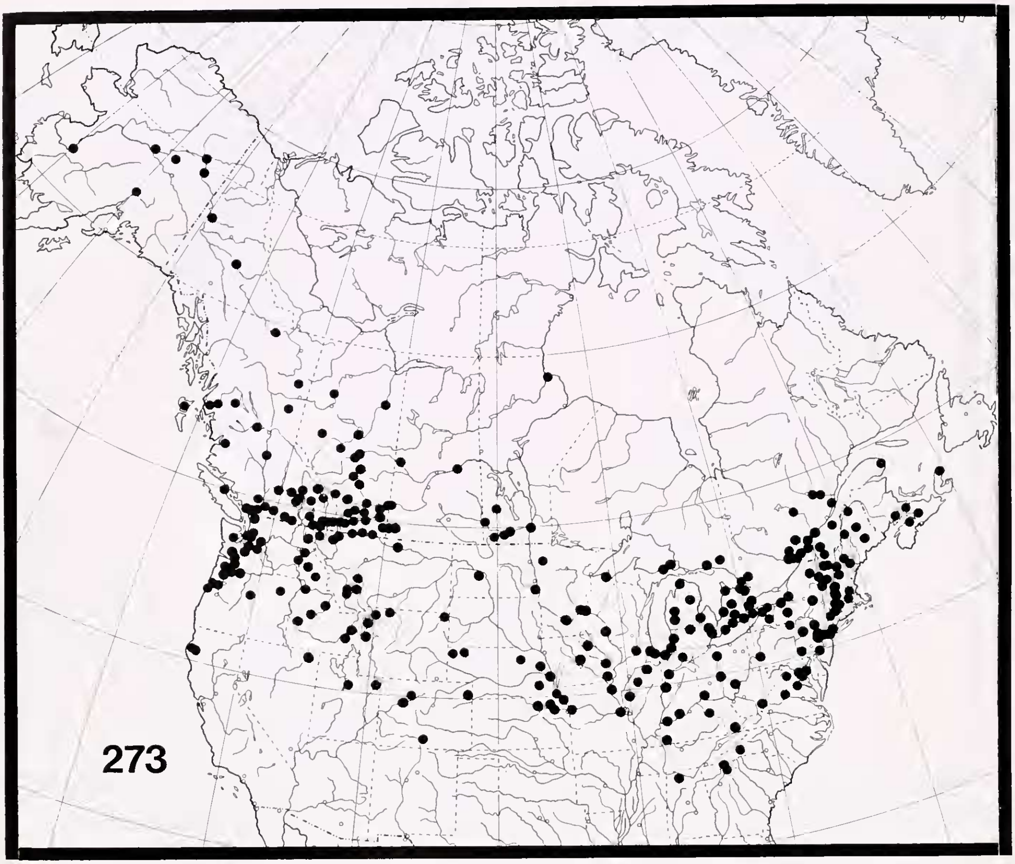
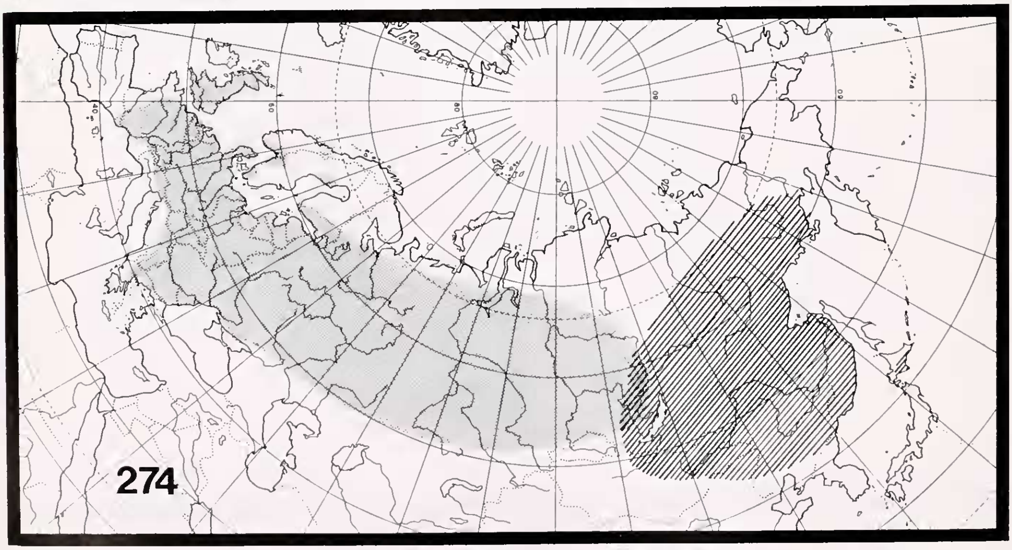


Figure 272. Geographic distribution of *B. levettei*. *B. levettei levettei* (stars) and *B. levettei carrianum* (dots). Localities of specimens identified using male genitalia indicated by larger symbols.





Figures 273, 274. Geographic distributions of species of *Bracteon*. 273. *B. inaequale*. 274. Approximate distributions of *B. litorale* (stippled) and *B. conicolle* (striped). Based on Lindroth (1962), Turin *et al.* (1977), and personal observations.

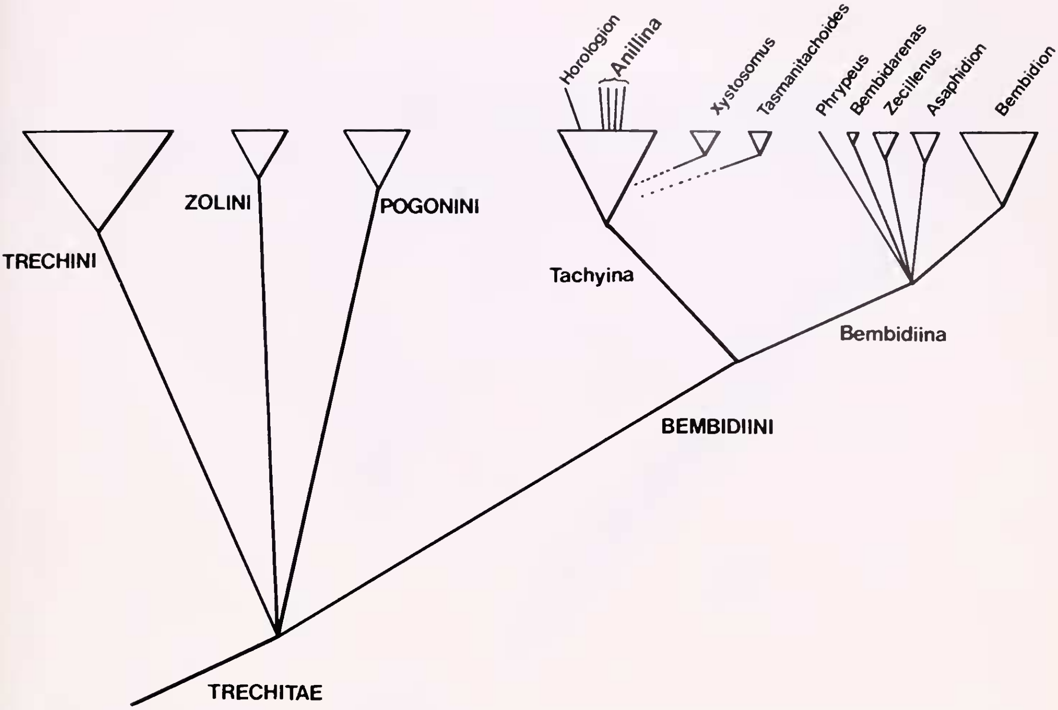
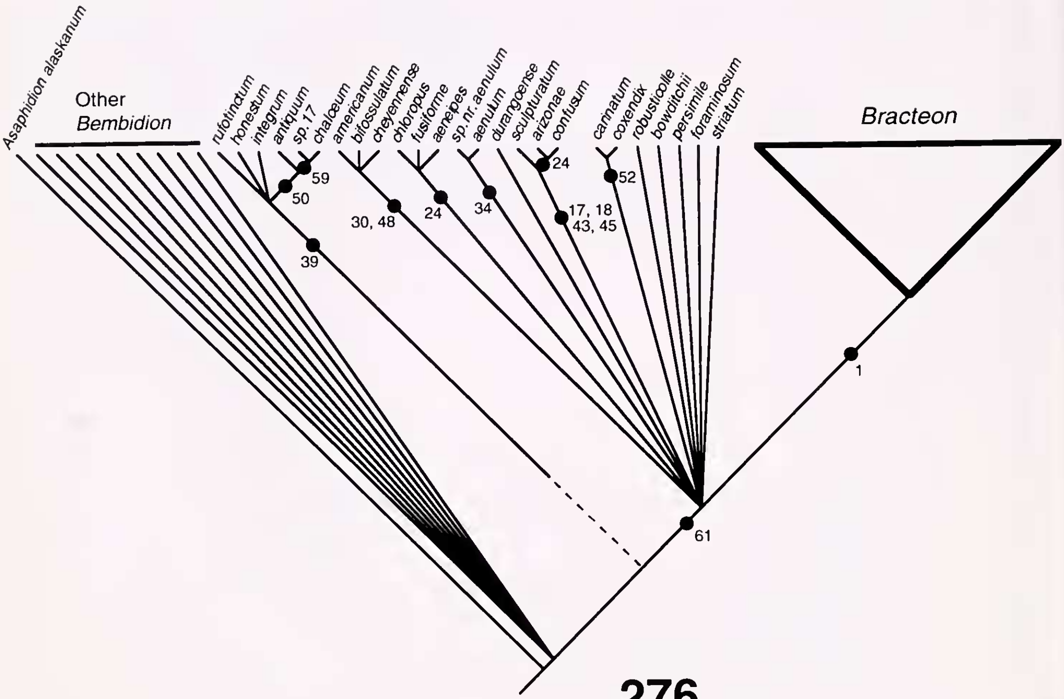
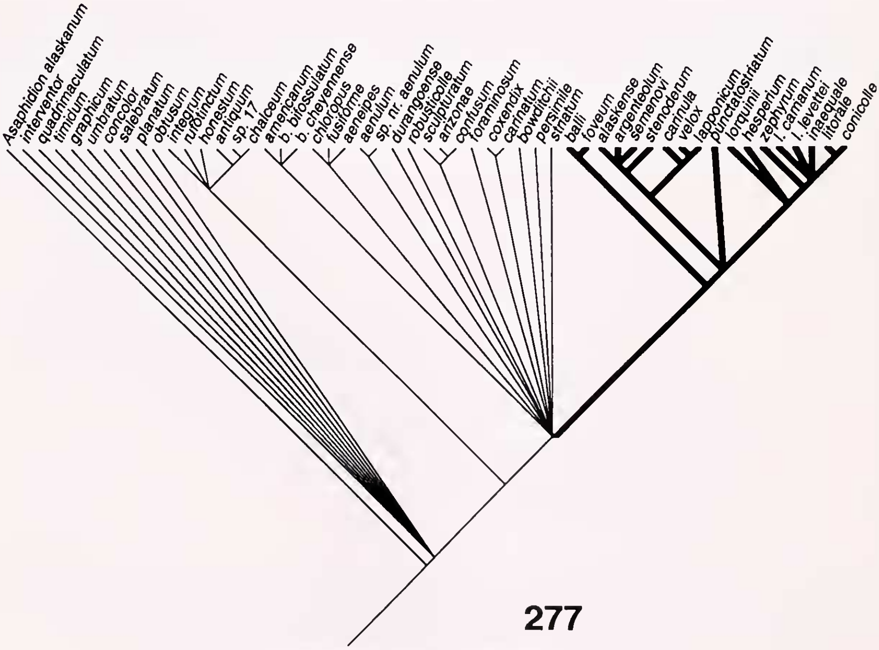


Figure 275. Proposed cladistic structure of Trechitae and genera of Bembidiina. Based mainly on Kryzhanovskij (1976) and Erwin (1972, 1982, and 1985).



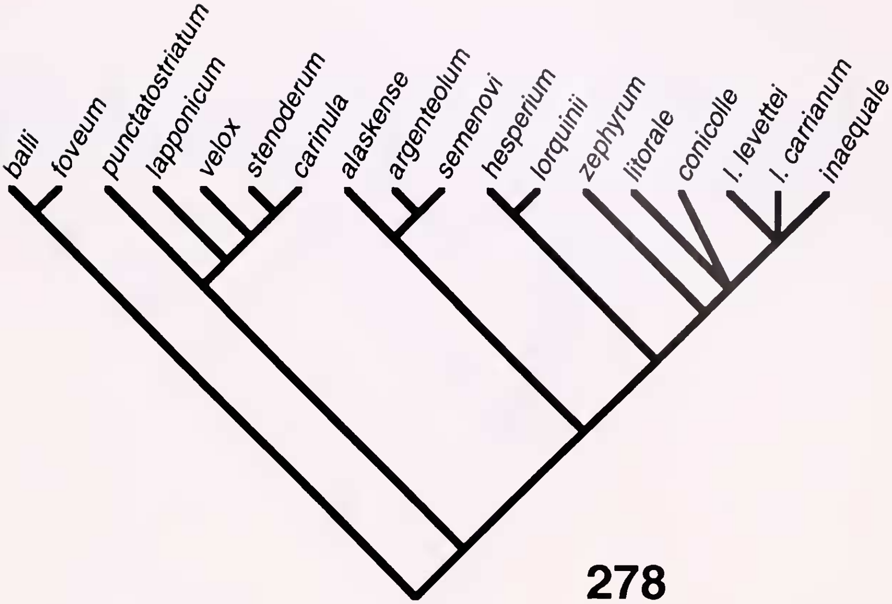
276

Figure 276. Cladistic structure of near relatives of *Bracteon*, based on traditional analysis. Numbers below a clade are the numbers of characters for which derived states support monophyly of the clade (see Tables 2, 4, and 5).

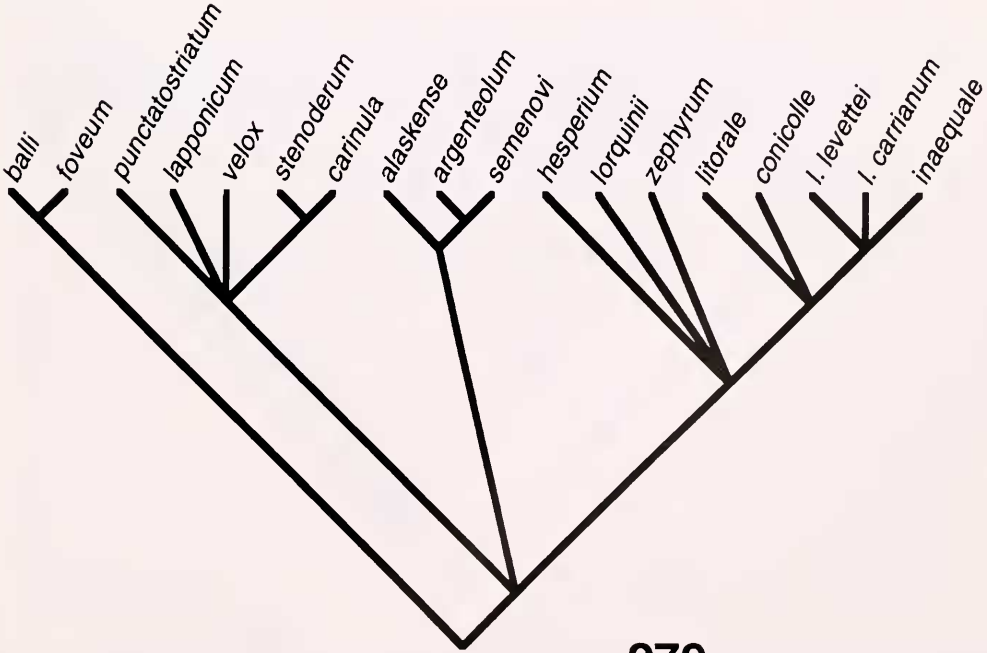


277

Figure 277. Phylogeny inferred from traditional analysis. *Bracteon* lineages are shown with thicker lines.

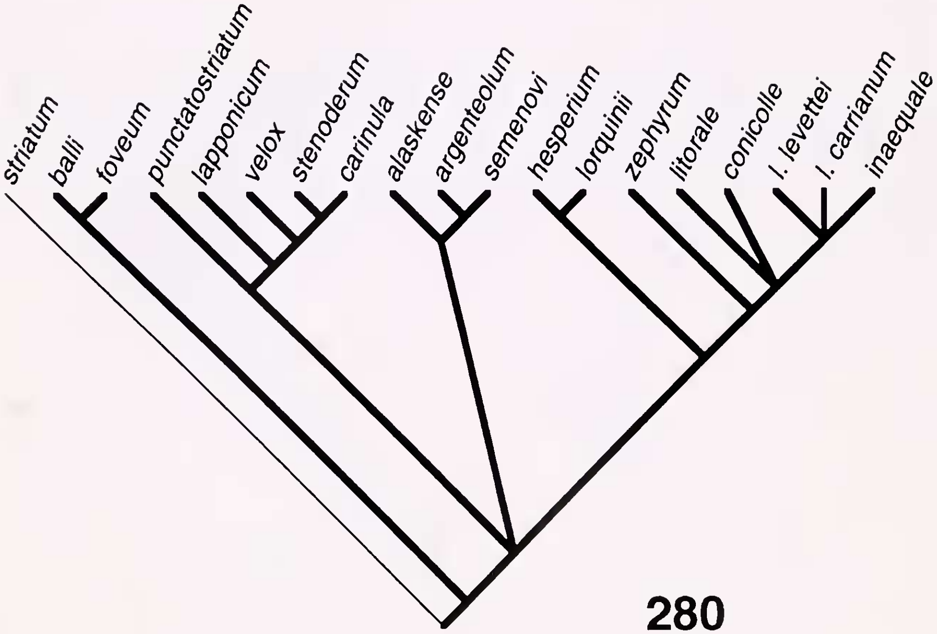


278



279

Figures 278, 279. Most-parsimonious trees of only the 18 *Bracteon* taxa. 278. Equal weighting. 279. Error-prone characters devalued.



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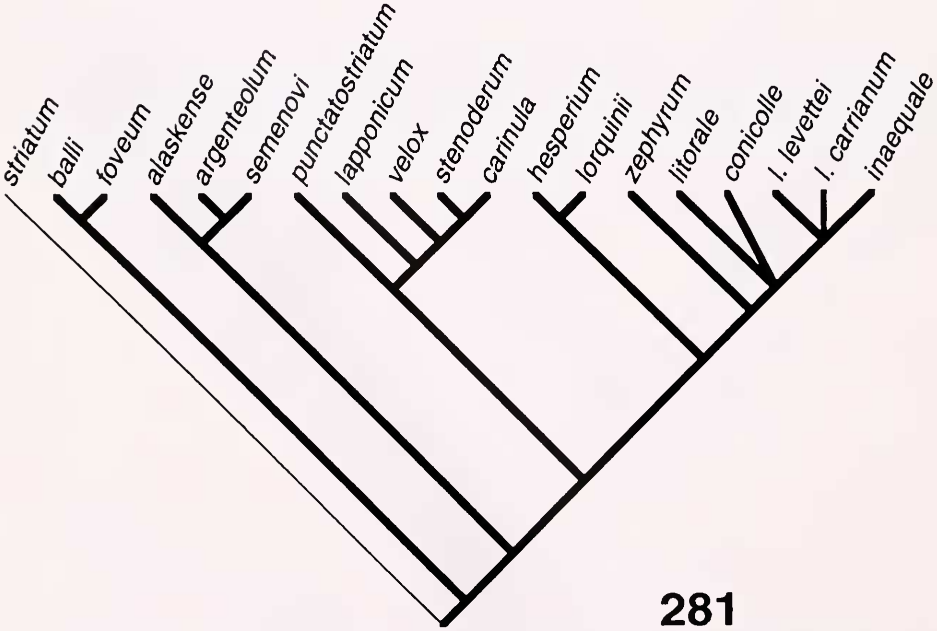
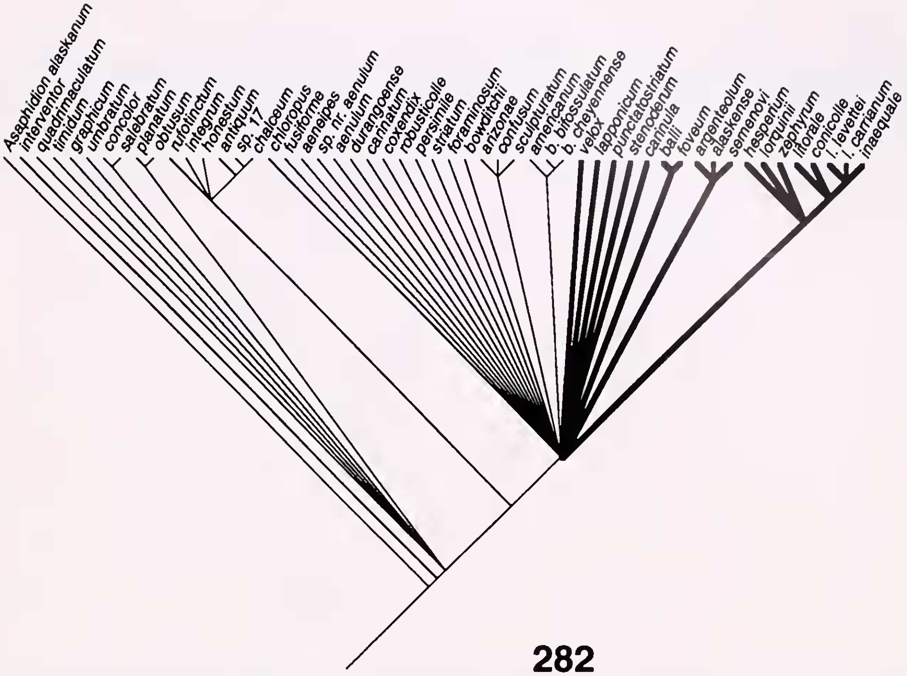


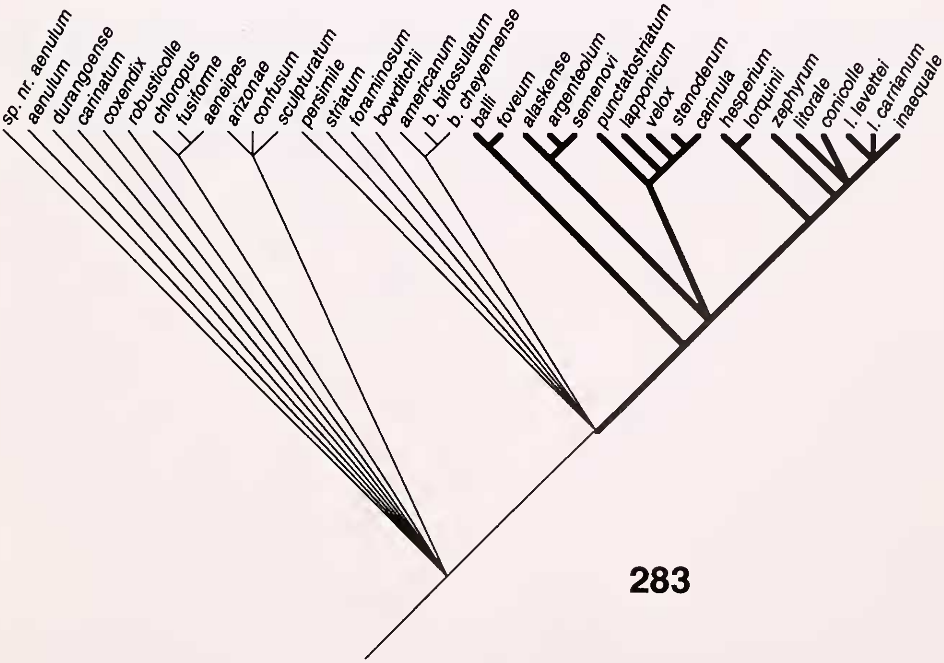
281

Figures 280, 281. Most-parsimonious trees of only the 18 *Bracteon* taxa plus *B. striatum*. 280. Equal weighting. 281. Error-prone characters devalued.



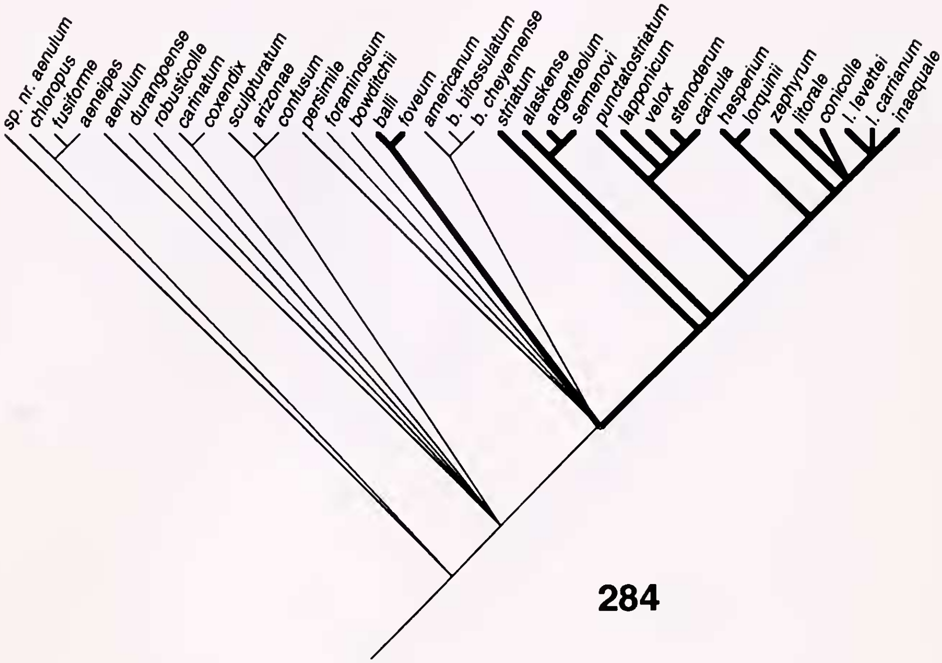
282

Figure 282. Strict consensus tree of all 545 most-parsimonious trees of length 653 found by PAUP; characters equally weighted.



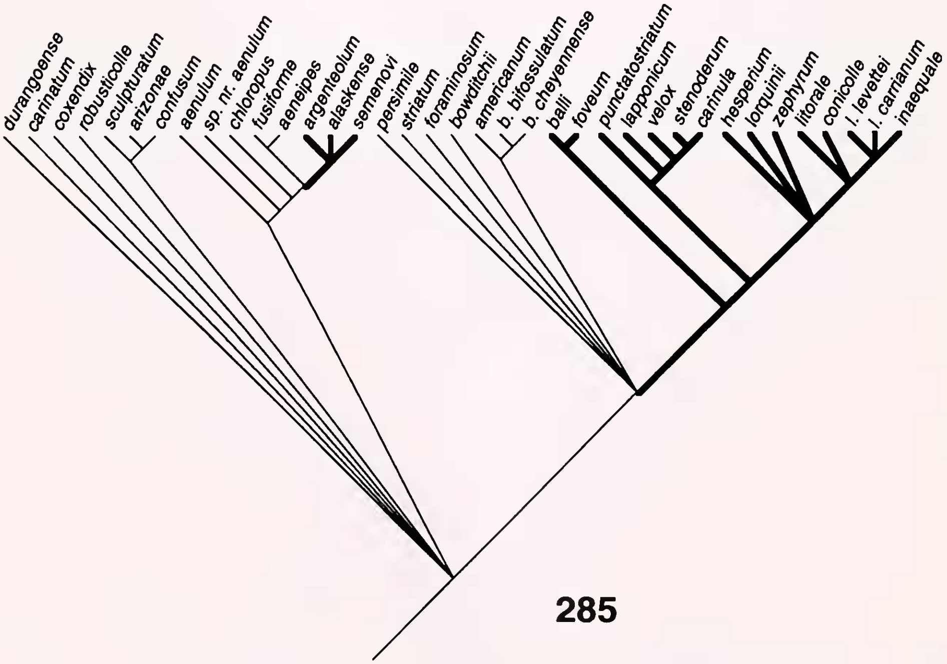
283

Figure 283. Part of the strict consensus tree of 140 trees of length 653 with *Bracteon* monophyletic.



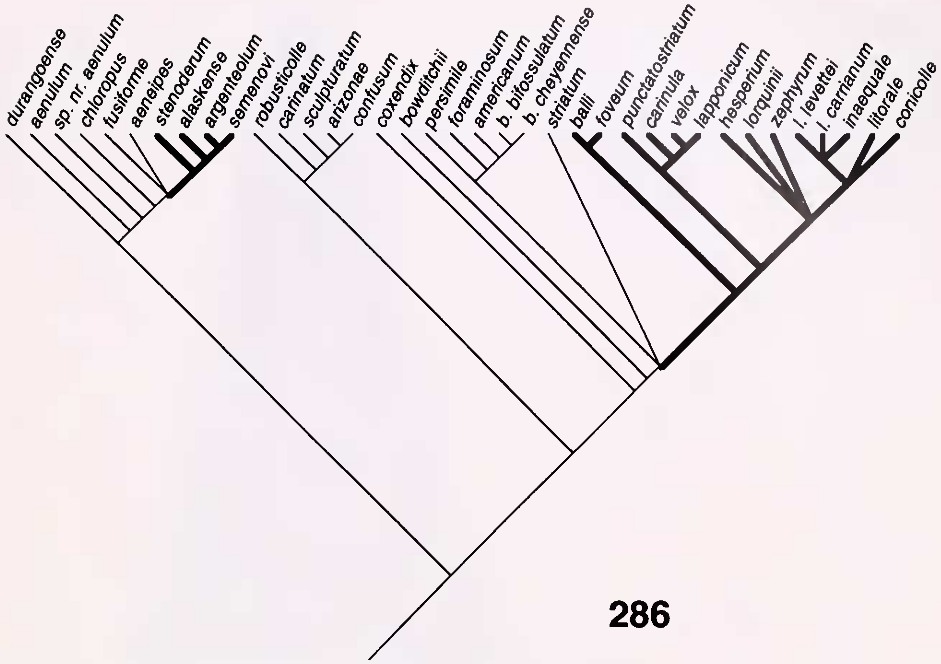
284

Figure 284. Part of the strict consensus tree of 88 trees of length 653 with *B. balli* and *B. foveum* excluded from *Bracteon.*



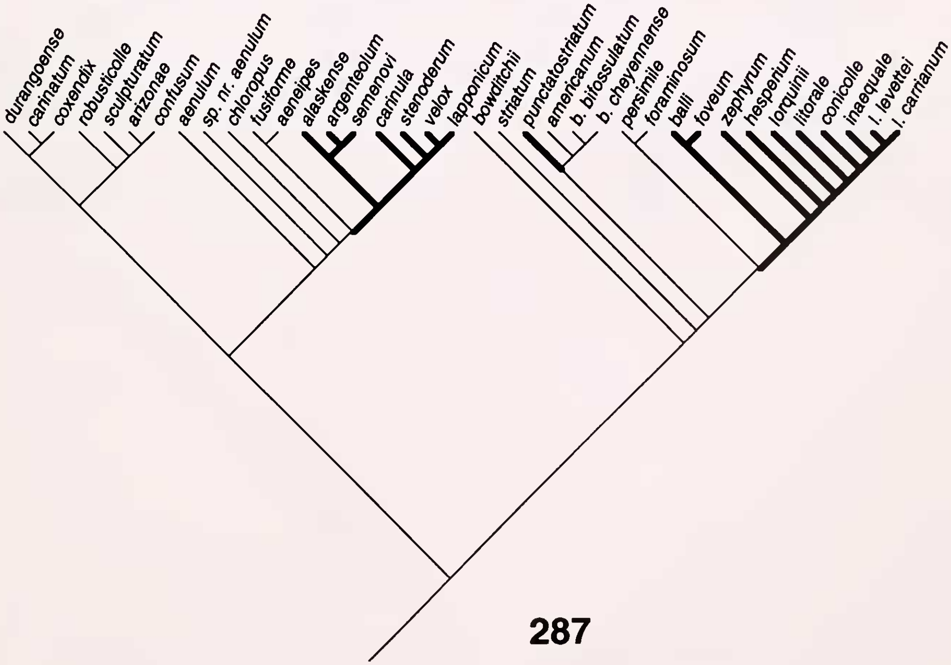
285

Figure 285. Part of the strict consensus tree of 268 trees of length 653 with the *B. argenteolum* group excluded from *Bracteon.*



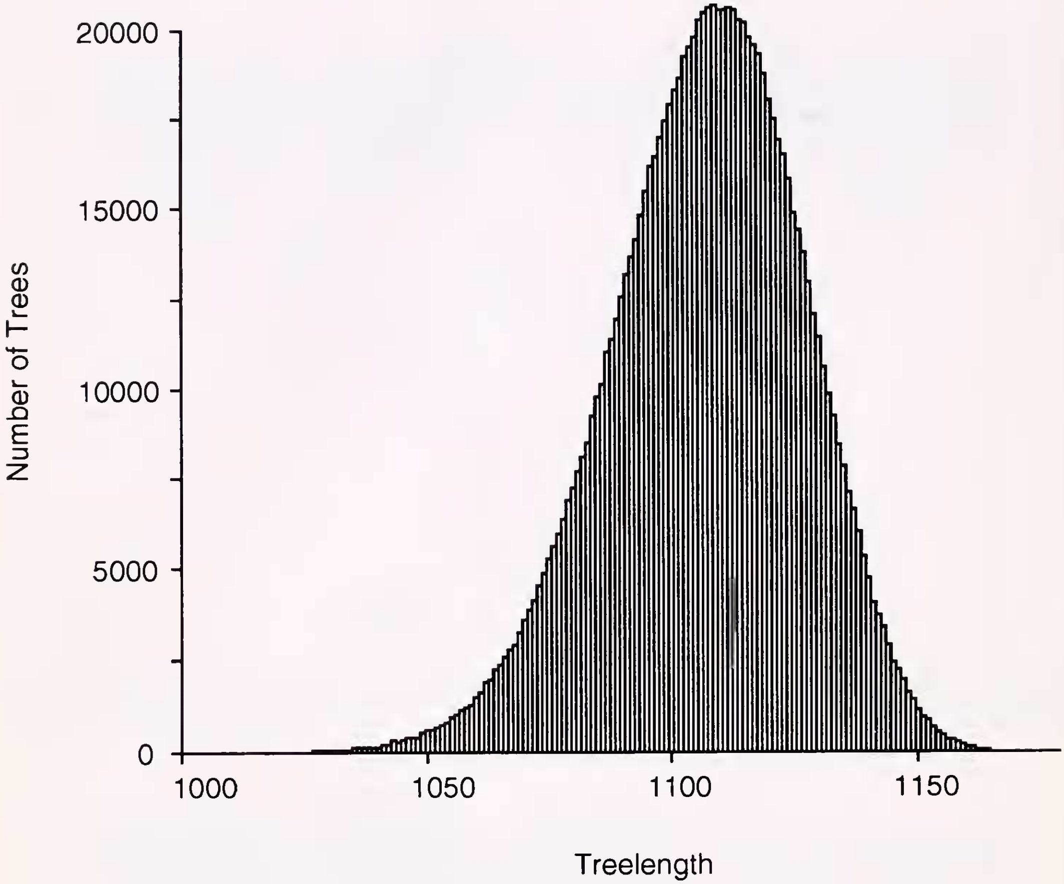
286

Figure 286. Part of the strict consensus tree of 48 trees of length 653 with the *B. argenteolum* and *B. stenoderum* group excluded from *Bracteon*.



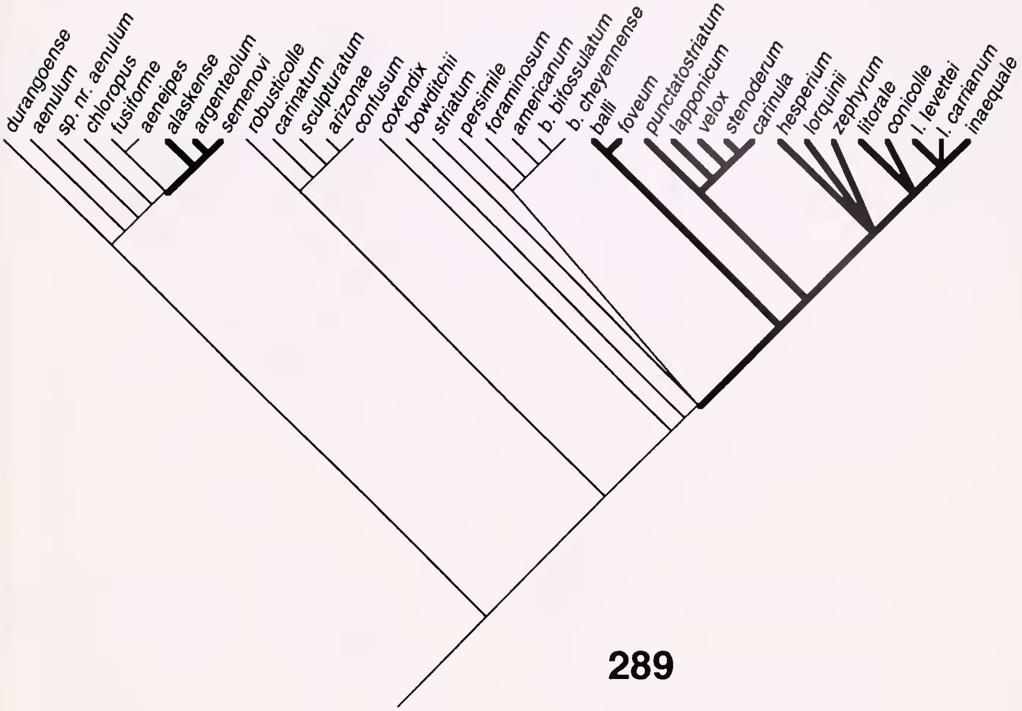
287

Figure 287. Part of the single tree of length 653 with *Bracteon* shattered into 3 clades.



288

Figure 288. Distribution of random sample of 1,000,000 equiprobable trees from full, unrecoded data set; characters equally weighted.



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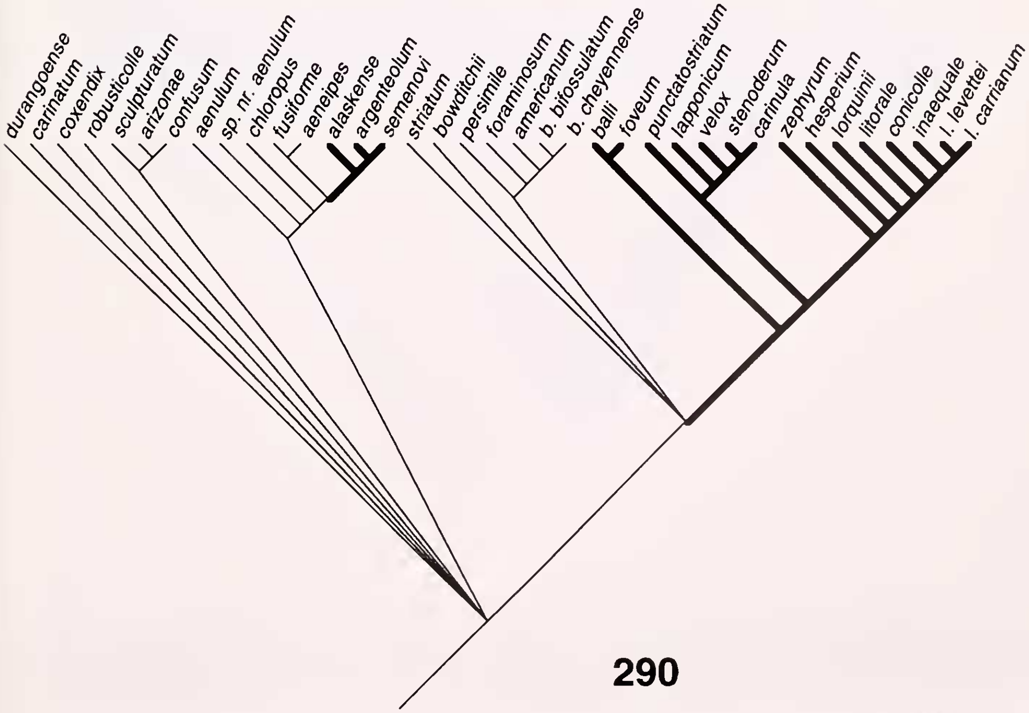
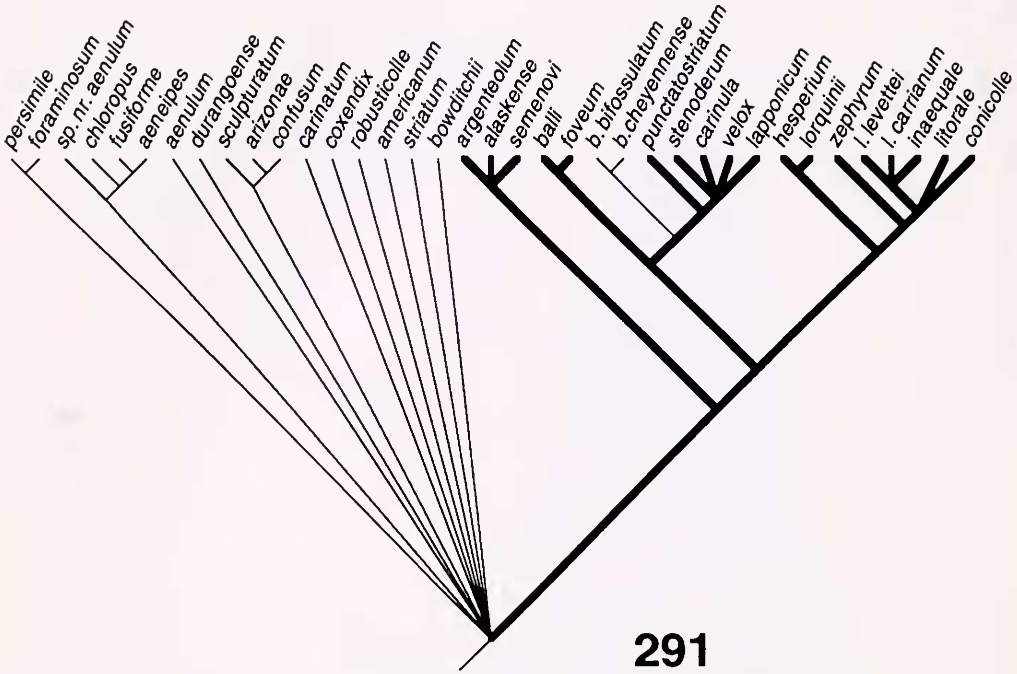


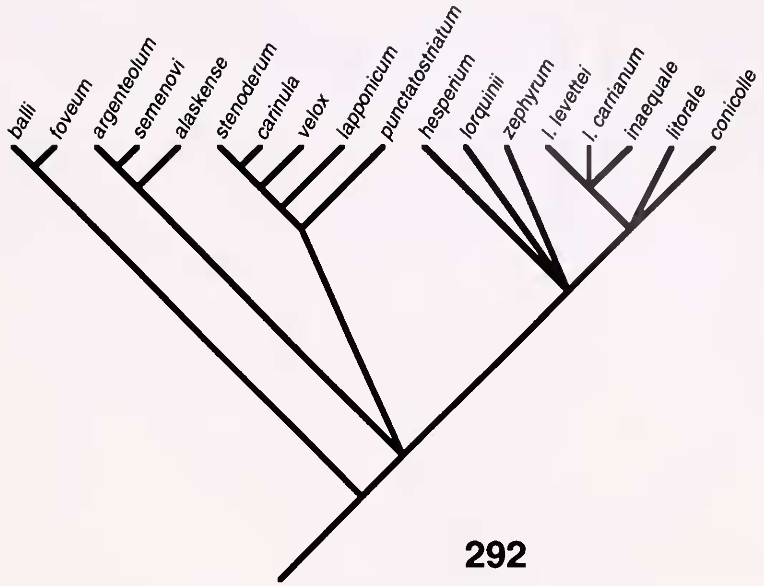
290

Figures 289, 290. Most-parsimonious trees under two weighting schemes. 289. Part of the strict consensus tree of 120 trees of length 1,086 with error-prone characters devalued. 290. Part of the strict consensus tree of 21 trees of length 1,406 with error-prone characters and extensively polymorphic characters devalued.



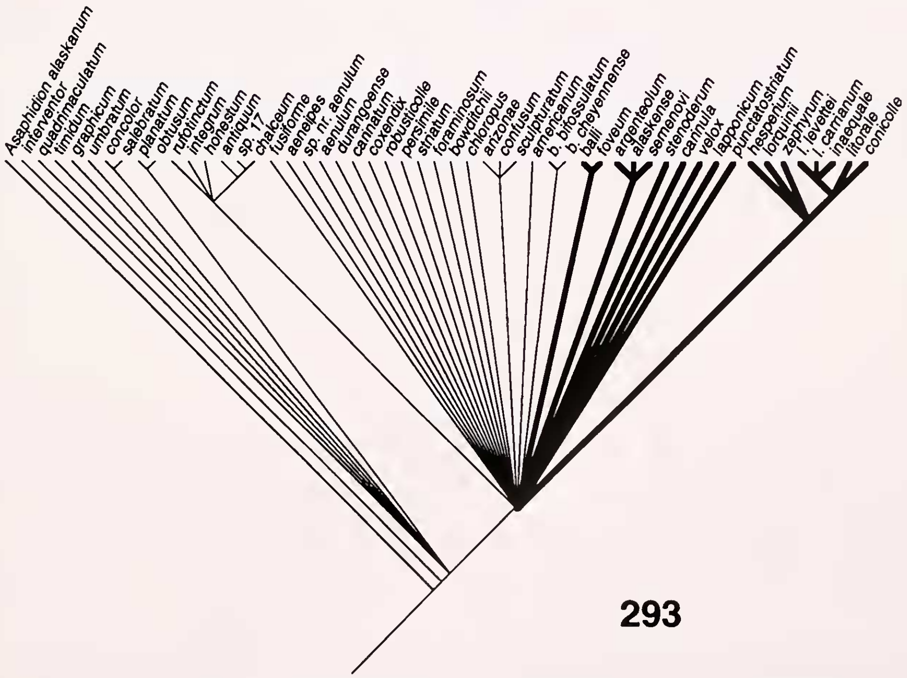
291

Figure 291. Part of the strict consensus tree of the island of 5,482 most-parsimonious trees for the matrix recoded so that inapplicable characters are not treated as missing data.



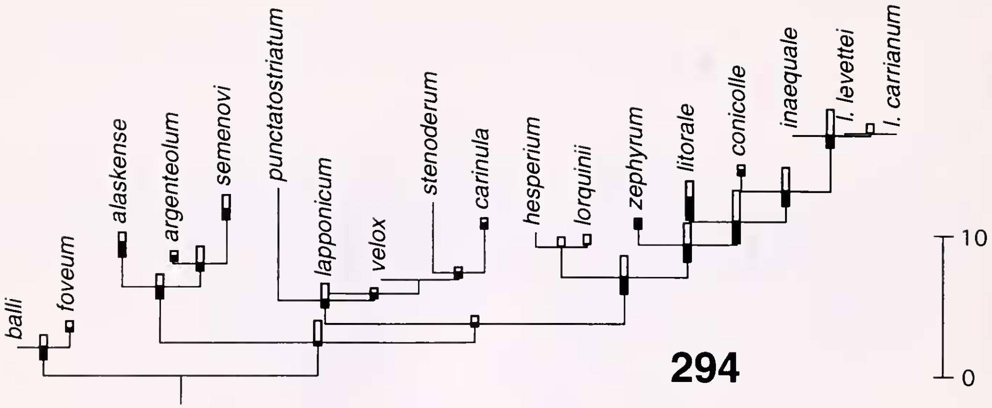
292

Figure 292. Part of the strict consensus tree of most-parsimonious trees under all three weighting schemes with the constraint enforced that *Bracteon* is monophyletic. Note that the structure shown here also matches that in Figures 278–281. This is the bold hypotheses of *Bracteon* relationships.



293

Figure 293. Strict consensus tree of most-parsimonious trees under all three weighting schemes, the most-parsimonious trees under the unequal weighting schemes in which *Bracteon* is forced to be monophyletic, and the most-parsimonious trees for the matrix recoded so that inapplicable characters are not treated as missing data. Under this cautious hypothesis, *Bracteon* is not presumed to be monophyletic.



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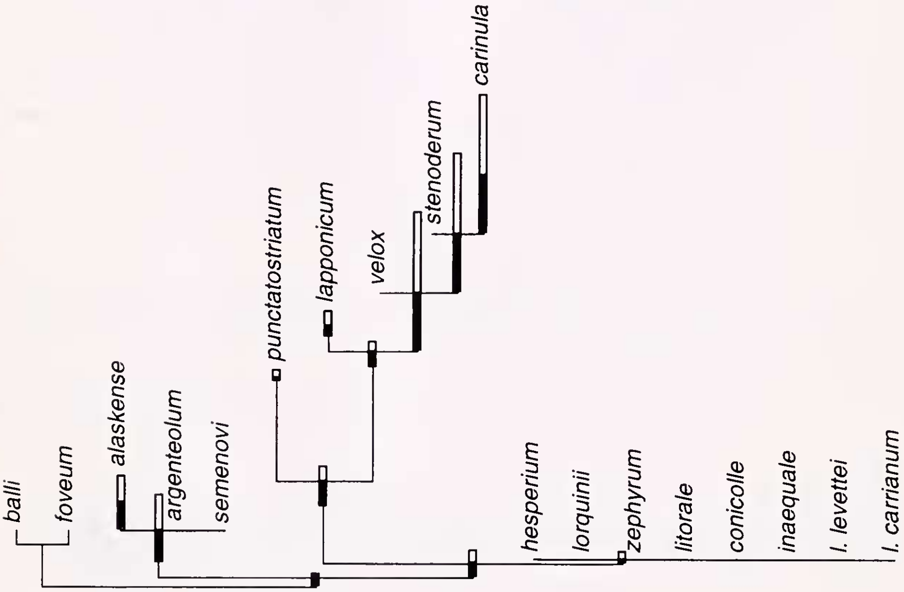

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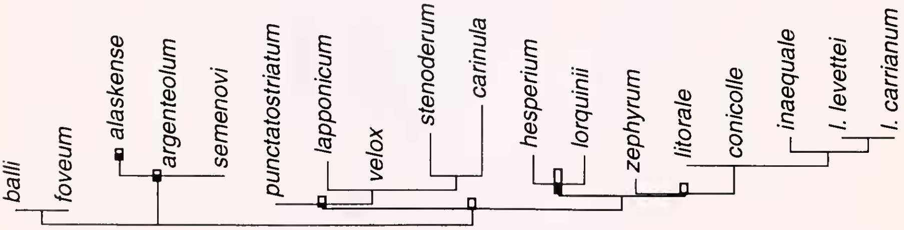
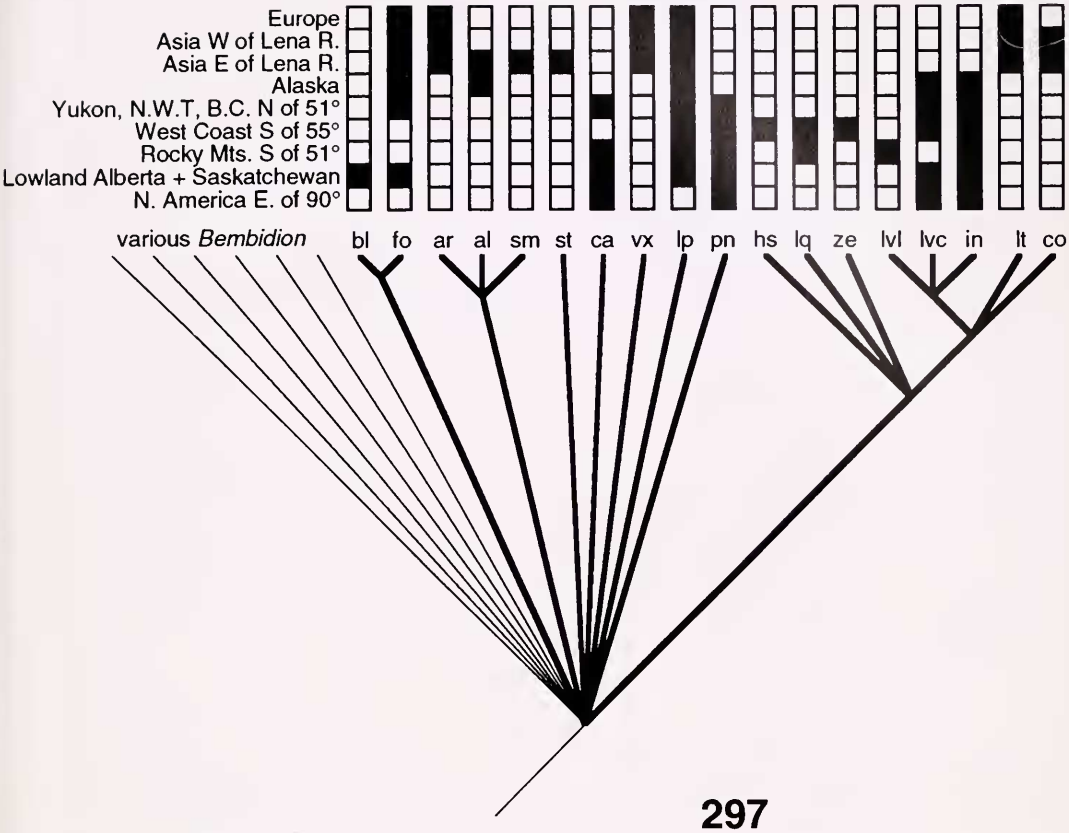


296

Figures 294–296. Distribution of evolutionary changes upon one of the four trees in common to the most-parsimonious trees for all three weighting schemes under the constraint that *Bracteon* is monophyletic. A dichotomous tree was chosen because of the difficulties in calculating branch lengths on polytomous trees (W. P. Maddison, 1989); this is thus a bolder hypothesis than is ideal. Branch length proportional to sum (over characters) of the average number of changes reconstructed by parsimony to occur on branch, where the average is taken over equally parsimonious reconstructions of character change for the character. The bottom of the black box on a branch indicates the sum (over characters) of the minimum number of changes reconstructed on that branch; the top of the white box indicates the sum (over characters) of the maximum number of changes reconstructed. 294. Adult external characters. 295. Larval characters. 296. Genitalic characters.



297

Figure 297. Geographic distributions of *Bracteon* species superimposed upon the cautious phylogeny. Abbreviations of taxon names as in Table 2.